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Fishery Bulletin

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166 Water Street
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Scientific Publications Office
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Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*

Steven E. Campana
Marine Fish Division, Bedford Institute of Oceanography
P.O. Box 1006, Dartmouth
Nova Scotia, Canada B2Y 4A2
E-mail: campanas@mar.dfo-mpo.gc.ca

Cynthia M. Jones
Applied Marine Research Laboratory and
Department of Biological Sciences
Old Dominion University
Norfolk, Virginia 23529-0456

Abstract.—Radiocarbon (^{14}C) in the world's oceans increased sharply between 1950 and 1970 as a result of the atmospheric testing of nuclear weapons. Through comparison with the ^{14}C time series reconstructed from atmospheric measurements and marine carbonates, Kalish, in 1993, used the ^{14}C concentration measured in fish otolith cores as a means of confirming the annulus-based age estimates for some South Pacific fish species. Here we report the pre- and postbomb ^{14}C chronology of North Atlantic adult black drum (*Pogonias cromis*), assumed to be between 15 and 42 yr of age on the basis of otolith annulus counts. According to accelerator mass spectrometry (AMS) assays, ^{14}C in otolith cores increased sharply between 1958 and 1964, with a timing and magnitude which was very similar to that of the atmospheric bomb ^{14}C signal. The correspondence between the two ^{14}C chronologies indicates that the annulus-based age assignments were accurate on average to within 1–3 yr. Differences between the black drum $\Delta^{14}C$ chronology and that of other marine carbonates in the North Atlantic are explained by the estuarine habitat of young-of-the-year black drum and by the fact that estuarine $\Delta^{14}C$ values more closely reflect atmospheric values than surface ocean values. At present, there is no other age-validation technique that can confirm the absolute age of long-lived fish species with comparable levels of accuracy.

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Despite the international acceptance of otolith annuli as the best means for estimating the age of most fish species, the correct interpretation of annuli is far from easy and can result in serious and systematic ageing errors (Beamish and McFarlane, 1995). Indeed, aside from the use of tagged, hatchery-reared fish released into the wild, confirmation of the accuracy of a method of annulus interpretation for marine fish species is often problematic. Mark-recapture of chemically tagged individuals has generally been considered to be the most accurate means of confirming the frequency of formation of presumed annuli, owing to a correspondence between time at liberty and the number of annuli distal to the chemical check (Foreman, 1996). Although the approach is sound, extremely low recapture rates for fish at liberty more than 2–3 years can make it difficult to acquire sufficient samples for an adequate test. Moreover, the technique validates the time elapsed since tagging, not the absolute age of the fish. Alternatively, radiochemical dating based on ^{210}Pb:^{226}Ra or ^{228}Th:^{228}Ra ratios can be used to differentiate between very different age interpretations (Bennett et al., 1982; Campana et al., 1990), but these assays are too imprecise for detailed or individual age confirmations. The most widely used approach, that of the seasonal progression of marginal increments (Beckman and Wilson, 1995) is well suited only to fast-growing fish and suffers from the lack of an objective means of evaluation. Thus there is a well-defined gap in our ability to confirm the age interpretations of the majority of marine fish species, particularly those that are long-lived. However, the recent finding that nuclear testing left a dated mark in the otolith (Kalish, 1993) provides a significant breakthrough in our ability to determine accurate, absolute ages for individual long-lived fish.

Kalish (1993) was the first to describe the use of bomb radiocarbon (^{14}C or carbon-14) as a dated marker in fish otoliths and its value for confirming age interpretations. His findings were based on earlier work that had documented a 100% increase in atmospheric radiocarbon as a result of the widespread atmo-

spheric testing of atomic bombs in the 1950's and 1960's (Nydal and Lovseth, 1983). This product of nuclear testing was subsequently incorporated into the world's oceans in a manner which has been well described at large spatial scales (Broecker et al., 1985; Duffy et al., 1995). Through analysis of annular growth rings in coral, other workers demonstrated that bomb radiocarbon was incorporated into the accreting coralline structure in concentrations proportional to those present in the water column (Druffel and Linick, 1978; Nozaki et al., 1978). Thus the time series of bomb radiocarbon in the coral was shown to reflect that present in the surface marine environment, which increased by about 20% between 1950 and 1970. Using accelerator mass spectrometry (AMS) as a sensitive and accurate assay tool, Kalish (1993) was able to demonstrate that the otoliths of a New Zealand fish species also incorporated ^{14}C and that the time series of radiocarbon reconstructed from the presumed otolith annuli was similar to that present in nearby corals. Thus he was able to infer that the otolith annuli had been interpreted and aged correctly because systematic under- or over-ageing would have resulted in a phase shift between the otolith ^{14}C and the coral ^{14}C time series.

Subsequent work by both Kalish (1995a, 1995b; Kalish et al., 1996) and Campana (1997) has confirmed the value of the bomb radiocarbon technique for solving problems of age validation in a variety of fish species. Furthermore, recent work by Campana (1997) has confirmed that the assumption of synchronicity between otolith and marine carbonate ^{14}C chronologies is justified, because the period of rapid increase in the ^{14}C chronology recorded in age-1 haddock (*Melanogrammus aeglefinus*) otoliths was synchronous with that reported for other taxa in the North Atlantic, whether based on corals (Druffel, 1989) or bivalves (Weidman and Jones, 1993). Such large-scale synchronicity implies that the ^{14}C time series reconstructed from the otolith cores of old fish can be compared to one of the other North Atlantic time series; errors in annulus-based age determinations would manifest themselves as noncoherent time series. The only constraint to such an age determination procedure is the requirement for otoliths of fish spawned during and adjacent to the 1958–65 period, so as to take advantage of the unique ^{14}C values during that period.

The black drum, *Pogonias cromis*, with its putative lifespan of some 60 yr and estuarine dependence during early life (Jones et al., 1997), is an ideal candidate for age validation with ^{14}C. This large sciaenid is distributed along the east coast of the U.S. (Jones et al., 1997) and throughout the Gulf of Mexico, where it is fished commercially. However its relatively low abundance results in low recapture rates after tagging. Accordingly, attempts to validate annulus formation with mark-recapture techniques in the older age groups have been unsuccessful. Yet such validation is critical to the proper management of this fish in the Chesapeake Bay region, where the greatest numbers of presumably old fish are harvested.

Here we report the first pre- and post[atom]bomb ^{14}C otolith chronology for black drum, and the first such chronology for any long-lived fish species in the North Atlantic. We use this ^{14}C chronology to determine the absolute ages of individual fish, and through comparison with otolith annulus counts from the same fish, we then confirm the accuracy of otolith annuli as indicators of absolute age in this species.

Materials and methods

Adult black drum (n=31) with a mean ±SE total length of 111 ±1 cm (range=95–119 cm) were collected with anchored and drifted gill nets during research surveys of the eastern shore of Chesapeake Bay in Apr–May 1990. To estimate age based on annuli, one randomly selected sagittal otolith of each otolith pair was sectioned transversely through the core, and the annuli were counted under reflected light. The radius of the presumed first annulus was confirmed through measurements of the dimensions of intact sagittae collected from young-of-the-year black drum, which indicated that the first annulus in a transverse section should be approximately 7 mm wide and 2 mm thick. After ageing with reflected light microscopy, the remaining halves of each otolith were stored dry in paper envelopes in preparation for ^{14}C assay.

To extract a sample of the first year's growth from each otolith, a transverse section 1-mm thick was made with an Isomet saw immediately adjacent to that made for ageing. Although this second section was adjacent to the otolith core, the length of the age-1 otolith (~8 mm) indicates that most of the first year's growth was still present in the section. After recording a digital image of the annuli, a Dremel tool was used to remove all otolith material distal to the first annulus. The remaining core material was then stored in aluminum foil and submitted for ^{14}C assay by AMS. All samples were also individually assayed for $\delta^{13}C$, which was used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as $\Delta^{14}C$, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977).

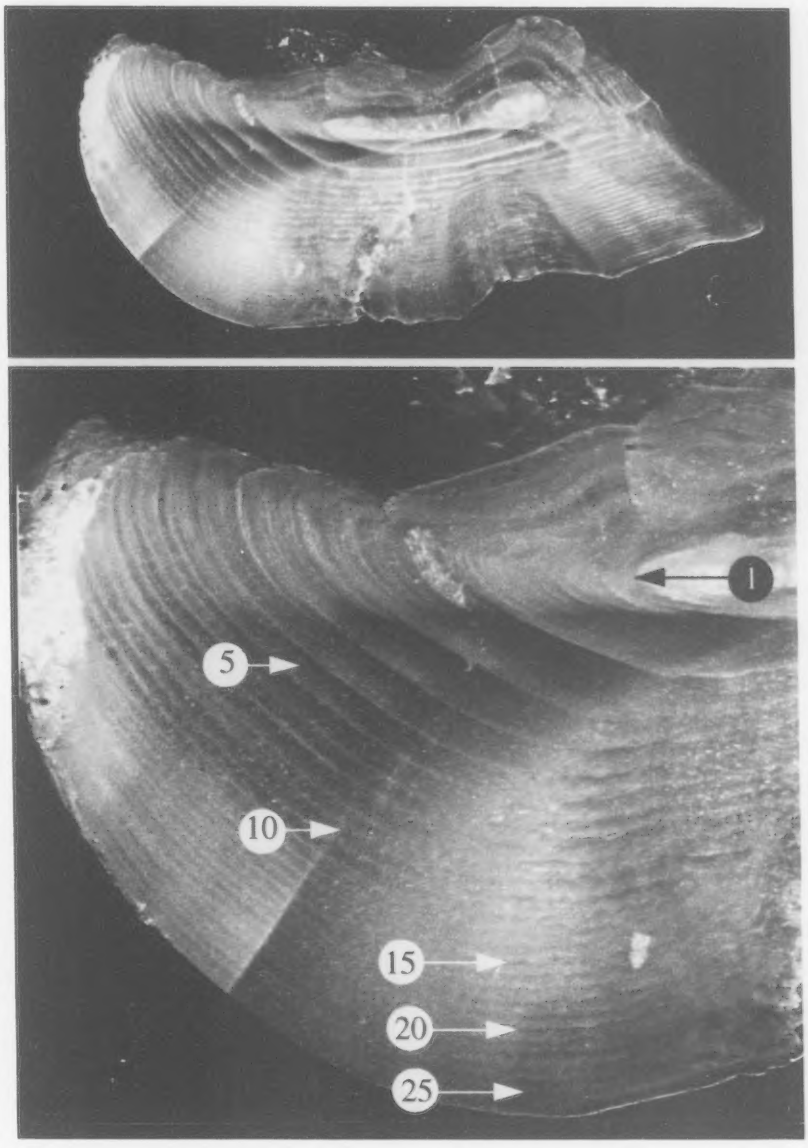

Figure 1

(A) Transverse section of an adult black drum otolith presumed to be 27 years old. **(B)** A magnified view of the ventral side of the sulcus, a region in which the annuli (indicated by arrows) tend to be most clear. Bar = 2 mm.

Results

The presumed annuli in the black drum otolith sections were clear and unambiguous (Fig. 1). Age bias plots (Campana et al., 1995) of the counts of the two independent age readers showed no bias and high precision (CV=1.6%) over an age range of 15–42 years. Although the number of annuli was generally consistent on both the dorsal and ventral sides of the sulcus, the latter was usually the clearer of the

two. Therefore, all age and year-class estimates were based on annulus counts along the ventral aspect of the core-medial axis.

The assay results for mean $\delta^{13}C$ were consistent with those observed previously in fish otoliths (mean ± SD=–3.48±1.50‰) (Table 1). Although the presence of a slight but significant decrease across years (b= –0.09, P=0.04, r^2=0.13) was somewhat larger than the long-term ocean trend reported by Quay et al. (1992) and was of different slope than that reported for North Atlantic haddock otoliths (Campana, 1997), the biological significance of the observed trend is questionable given the relatively large coefficient of variation (CV=43%) among the samples. In contrast, $\Delta^{14}C$ differed strongly and systematically though time; concentrations were relatively low and constant prior to the late 1950's but increased sharply to a peak in the mid-1960's (Table 1; Fig. 2). Subsequent values continued to decline to the end of the time series in 1975. The maximum rate of increase occurred between 1958 and 1964 and was easily differentiated from the adjacent time periods. Therefore, the $\Delta^{14}C$ of the cores of the black drum otoliths was characteristic of the period of incorporation and could reasonably be considered a dated marker.

Table 1

Summary of $\Delta^{14}C$ and $\delta^{13}C$ assay results for each black drum otolith core.

Year class	Annulus age (yr)	$\Delta^{14}C$	SD	$\delta^{13}C$
1948	42	–38.8	5.9	–0.9
1950	40	–78.2	8.3	–2.7
1952	38	–36.7	6.4	–2.4
1954	36	–71.9	5.9	–5.9
1954	36	–62.8	6.1	–2.1
1957	33	1.9	4.6	–2.7
1958	32	45.2	7.8	–2.2
1959	31	–3.1	6.4	–3.0
1959	31	101.9	7.2	–1.9
1960	30	46.1	6.8	–3.3
1960	30	18.1	6.6	–4.3
1960	30	70.8	6.8	–1.9
1961	29	175.3	7.5	–3.3
1962	28	62.4	4.5	–5.9
1962	28	182.5	7.5	–4.4
1963	27	299.3	8.5	–0.8
1963	27	136.2	7.3	–2.6
1963	27	95.7	7.1	–5.8
1964	26	111.4	6.8	–6.0
1964	26	194.2	7.6	–2.3
1964	26	371.4	9.1	–4.8
1965	25	340.6	8.6	–4.4
1965	25	106.4	7.1	–4.9
1966	24	366.5	9.1	–4.4
1967	23	291.1	8.5	–3.3
1968	22	297.2	10.2	–2.9
1968	22	261.8	8.2	–2.9
1968	22	207.5	8.0	–3.2
1970	20	213.1	7.8	–2.4
1973	17	255.2	8.1	–4.0
1975	15	150.4	6.5	–6.3

The $\Delta^{14}C$ from the otolith cores from the prebomb, pre-1957 year classes (–57.7±19.0‰) was very similar to that which has been measured in other North Atlantic otoliths, corals, and bivalves (Fig. 3). However, considerably more ^{14}C was incorporated into black drum otoliths during the 1960's than has been measured in most other marine carbonates. Indeed, peak $\Delta^{14}C$ values in black drum (~340‰; Fig. 2) were almost twice as high as those recorded in contemporaneous corals, and almost four times as high as those measured in haddock otoliths of the same year classes. After normalizing the black drum and marine carbonate time series to the same scale, the black drum $\Delta^{14}C$ chronology appeared to both begin its increase and reach a peak approximately 2–3 yr before that of the other carbonates. In addition, unlike the $\Delta^{14}C$ in the other taxa, the $\Delta^{14}C$ in the black drum otoliths declined significantly (to +150‰ in 1975) after reaching a peak in the mid-1960's. Thus in terms of phase coherence, peak magnitude, and subsequent decline, the black drum $\Delta^{14}C$ chronology more closely resembled that of the atmosphere than of other marine carbonates.

To assess the level of correspondence between the black drum $\Delta^{14}C$ chronology and that of the atmosphere, the two time series were scaled to comparable magnitudes. The resulting correspondence was striking (Fig. 4), both in its rate of increase and subsequent decline. The phase shift between the two chronologies was approximately 1 yr, with black drum lagging behind atmosphere.

Discussion

In light of the sharp rate of increase of the ^{14}C signal associated with the onset of nuclear testing, interpretation of the ^{14}C chronology in otolith cores is relatively simple; the otolith chronology should match other published chronologies for the region as long as the annular age assignments (=year class) are correct. Any under-ageing would phase-shift the otolith ^{14}C chronology towards more recent years, whereas over-ageing would phase-shift it towards earlier years. Because marine waters with $\Delta^{14}C$ values greater than 0‰ did not generally exist prior to the late 1950's, coastal fish otolith cores with subzero values must have formed before the late 1950's. Contamination with material of more recent origin

could only increase the $\Delta^{14}C$ value, not decrease it. Thus the $\Delta^{14}C$ value sets a minimum age for the sample, and the years 1958–65 become the most sensitive years for $\Delta^{14}C$-based ageing. It is on this basis that workers in other disciplines have used bomb radiocarbon assays to infer age and the frequency of growth-ring formation in both bivalves (Turekian et al., 1982; Peck and Brey, 1996) and mammals (Bada et al., 1990).

The coherence between the otolith-based ^{14}C time series reconstruction reported here and that reported elsewhere in the North Atlantic for bivalves (Weidman and Jones, 1993), corals (Druffel, 1989), and haddock otoliths (Campana, 1997) indicates that black drum age assignments were, on average, reasonably accurate (Fig. 3). The similar prebomb $\Delta^{14}C$ histories for these taxa reflect a common baseline value, whereas differences in post-1970 histories reflect geographic variability in water mixing times (Weidman and Jones, 1993). However, the differences in phase, magnitude, and postbomb decline among the various $\Delta^{14}C$ chronologies are both significant and meaningful and suggest that more accurate age interpretations may be possible. To improve ageing accuracy, however, three additional assumptions must be met: 1) the extracted otolith core must not be contaminated with material of more recent origin; 2) annulus interpretations and any associated errors must be made consistently across all ages examined; 3) the ^{14}C "reference" chronologies must be synchronous with that of the fish species under study. The first assumption has only been tested by Campana (1997) for haddock but was found to hold in part; intact age-1 otoliths and the extracted core of older fish from the same year class were characterized by similar $\Delta^{14}C$ values, although there was a tendency for more recent $\Delta^{14}C$ values to be found in the older cores, suggesting limited contamination. The second assumption is implicit in all ageing studies, because it implies that a given growth increment is interpreted in the same way, whether observed in a young or an old fish. However, the third assumption, that of synchronicity among all North Atlantic ^{14}C chronologies, is more interesting. This assumption has been tested and found to hold in all ^{14}C

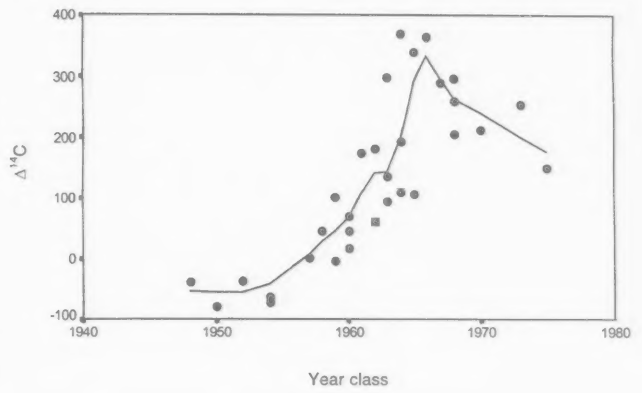

Figure 2

$\Delta^{14}C$ in the otolith cores of adult black drum in relation to the year class estimated from counts of presumed annuli. The $\Delta^{14}C$ values have been fitted with a LOWESS curve.

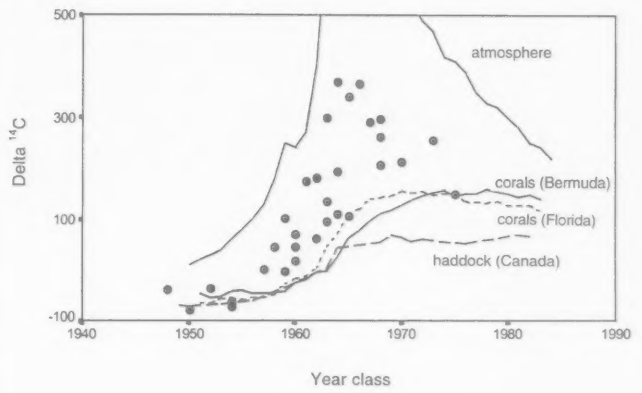

Figure 3

$\Delta^{14}C$ values in the otolith cores of adult black drum in relation to published $\Delta^{14}C$ chronologies for the atmosphere, corals from Bermuda and Florida, and haddock otoliths from eastern Canada. Whereas peak $\Delta^{14}C$ values differed among the time series, all shared a similar period of increasing values, with the source of the ^{14}C (the atmosphere) predating the coral and haddock time series by 2–4 years. The black drum chronology lies intermediate in phase and value to the atmospheric and marine carbonate time series, reflecting an estuarine origin. The two coral chronologies are drawn from Druffel (1989), and the chronologies for the atmosphere and haddock are from Nydal (1993) and Campana (1997), respectively.

otolith ageing studies reported to date, whether in the North Atlantic (Fig. 3) or in the South Pacific (Kalish, 1993, 1995a, 1995b; Kalish et al., 1996). However, the $\Delta^{14}C$ chronology reconstructed from the black drum otoliths was noticeably different; whereas prebomb ^{14}C values were comparable among all taxa, all postbomb year classes of black drum were significantly higher than those observed in any other open-ocean carbonate, and appeared to be phase-shifted 2–4 yr towards earlier years. This difference cannot be explained on the basis of ageing error, because the peak $\Delta^{14}C$ values in the otolith were as much as four times higher than those recorded in any year of any other open-ocean species. However, the apparent anomaly is fully explicable when the life history of the black drum is considered. The black drum is a marine fish but spends the first year of its life in rivers or estuaries (Richards, 1973). Thus the elemental and isotopic composition of the otolith core reflects the riverine or estuarine environment, not that of the open ocean. Because estuaries are shallow, well-mixed areas with strong riverine input, there is a rapid and relatively complete exchange of radiocarbon between the atmosphere and the water. As a result, the ^{14}C chronology of an estuary is a much closer reflection of the atmospheric chronology than of the marine chronology (Erlenkeuser, 1976; Spiker, 1980; Tanaka et al., 1986). Thus it is to be expected that the $\Delta^{14}C$ values of the black drum otolith core would lie intermediate, in magnitude and phase, to those of the atmosphere and the marine series, although closer to the former. This is indeed what was observed; thus black drum age assignments based on annular counts appear to be considerably more accurate than was originally thought, and not biased by 2–4 yr as would have been indicated by comparison with the marine carbonate chronologies. Nonetheless, the black drum measurements are the first demonstration of this phenomenon in fish and confirm Kalish's (1995b) suggestion that precise age calibrations against bomb radiocarbon signals must take into account the nature of the habitat in which the young fish has lived.

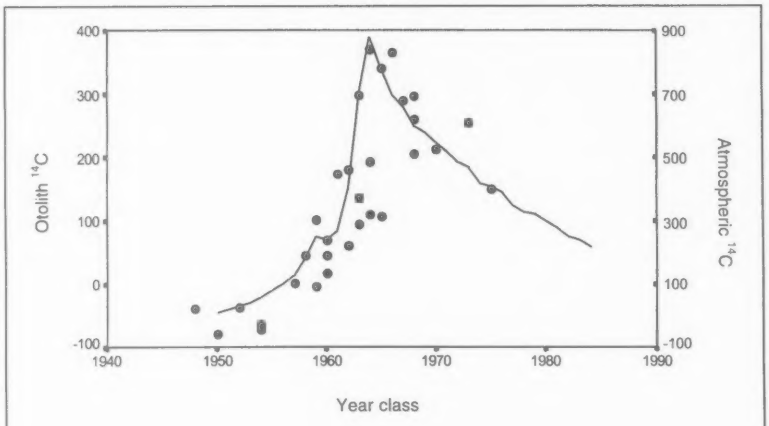

Figure 4

$\Delta^{14}C$ values in the otolith cores of adult black drum in relation to the published $\Delta^{14}C$ chronology for the atmosphere (data from Nydal [1993]). The data have been scaled so as to emphasize the similarities in the rate of increase and decline in the two time series. Otolith cores formed in riverine or estuarine waters would be expected to reflect more closely the atmospheric pattern of $\Delta^{14}C$ than that found in marine carbonates.

Whereas the the collection of black drum cores provided an unambiguous view of the period of $\Delta^{14}C$ increase, individual variability within any given year class was large and greatly exceeded the analytical error of the ^{14}C assays. Individual ageing errors undoubtedly contributed to this variability because even a 1-yr ageing error (in a 30-yr-old fish) would have resulted in a $\Delta^{14}C$ change of about 40 during the early 1960's. A similar argument applies to errors associated with the isolation of the otolith core from the surrounding, more recent, material. However, we believe that environmental heterogeneity and estuarine food sources were the dominant source of variability in the year-class-specific measurements. Variability in the isotopic composition of estuarine waters can be much larger than that of the open ocean: Spiker (1980) documented nearly twofold variability in the $\Delta^{14}C$ of total dissolved inorganic carbon (DIC) among locations in the Chesapeake Bay nursery area of black drum. The potential for variability due to diet in an estuary is also large. Because terrigenous carbon sources reflect atmospheric (enriched) $\Delta^{14}C$ in their isotopic composition and because terrigenous input and $\Delta^{14}C$ tend to decrease with increasing salinity, the isotopic composition of an animal's diet is bound to be more variable in an estuary than in a more homogeneous environment like the open ocean. Approximately half of the carbon incorporated into the shells of estuarine bivalves is derived from ^{14}C-enriched metabolic (dietary) sources, as opposed to DIC, with the result that there is a high variability among individuals (Erlenkeuser, 1976; Tanaka et al., 1986). Similar arguments undoubtedly apply to fish otoliths because metabolic

carbon is thought to provide about one third of the carbon to the otoliths (Kalish, 1991; Schwarcz et al., 1998).

Although the ^{14}C assays reported here provided absolute age determinations for black drum between the ages of 15 and 42 yr, they were of greater value for their use in confirming the accuracy of the criteria generally used to interpret otolith annuli. Compared with otoliths of many other fish species, black drum otoliths form remarkably clear annuli; thus it would have been somewhat surprising if their interpretation had proven to be incorrect. Indeed, on the basis of marginal increment analysis, an annual rate of otolith annulus formation has already been demonstrated for black drum (Beckman et al., 1990), as well as for the closely related red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991). An annual rate of formation has also been reported for annuli in young black drum scales (Matlock et al., 1993), despite the fact that scale annuli indicate a maximum age of only 10 yr for black drum in Chesapeake Bay. In any event, confirmation of the frequency of annulus formation cannot be used to infer absolute age with the same accuracy as a direct measure of absolute age. In light of the statistical uncertainty around the correspondence between the black drum ^{14}C chronology and that expected of an estuary, it appears reasonable to conclude that otolith annuli can be used to determine the age of a sample of black drum with an accuracy of at least ±1–3 yr, corresponding to 3–7% for a collection of 40-yr-old fish. The confidence interval for an individual fish would be, of course, somewhat larger.

Although techniques such as the mark-recapture of chemically tagged fish can be used to validate the annual frequency of formation of growth increments in the otolith accurately , especially in young or abundant fishes, only radiocarbon from nuclear testing has the potential to confirm both annulus formation and absolute age in individual fish. The results of this study suggest that bomb radiocarbon can be used to determine the accuracy of an alternative ageing technique to within 1–3 yr. In addition, the presence of a strong phase coherence across a broad array of organisms and areas has excellent implications for the age determination of other North Atlantic fish species. The only constraints to this procedure are the relatively high costs (~$700–$1,000 per otolith) and the requirement for fish hatched during the 1958–65 period, so as to take advantage of the unique ^{14}C values during that period. Although the availability of suitable otolith samples may limit the applicability of this approach to specific stocks and species, use of bomb-derived radiocarbon as a dated otolith marker appears to provide one of the most accurate and logistically feasible methods for age validation that is currently available.

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Discerning patterns in patchy data: a categorical approach using gulf menhaden, *Brevoortia patronus*, bycatch

Janaka A. de Silva
Department of Oceanography and Coastal Sciences
Louisiana State University
Baton Rouge, Louisiana 70803
E-mail address:Jandesilva@worldnet.att.net

Richard E. Condrey
Department of Oceanography and Coastal Sciences
Coastal Fisheries Institute, Louisiana State University
Baton Rouge, Louisiana 70803-7503

Abstract.—We use two categorical techniques to explore patchy data on releasable bycatch in the U.S. Gulf of Mexico menhaden fishery. With no previous statistical studies on releasable bycatch, this paper serves both as an analysis of patchy data with categorical techniques and as a quantitative description of a biologically important portion of the menhaden bycatch.

By means of exploratory analyses with loglinear and logit models, we determined spatial and temporal patterns in bycatch of the menhaden fishery. Contrasts revealed that at fishing grounds east of the Mississippi River, the probability of observing fishing sets with high bycatch rates in spring and summer were greater than in the fall. Furthermore, spring bycatch rates were higher in fishing areas east of 89°W than in fishing areas west of 93°W.

Correspondence analysis indicated that the fate of the releasable bycatch could be classified into three major groupings. The first group, species associated with being gilled, was composed primarily of *Micropogonias undulatus, Trichiurus lepturus, Chloroscombrus chrysurus,* and *Cynoscion arenarius.* The second group consisted of species associated with being dead or disoriented; it included the requiem sharks *Caranx hippos* and *Sciaenops ocellatus.* The third group included those fish that were associated with being put into the hold, those kept by the crew, or those whose fate was unknown. These included *Arius felis, Bagre marinus,* and *Scomberomorus maculatus.*

Seasonal and spatial associations of bycatch species were also examined with correspondence analysis. From April through August, two distinct bycatch species assemblages were observed that separated the fishery at a longitude of 91°W. From September through October, a shift in the species assemblage indicated that the western region of the fishery (west of 93°W) appeared to have a assemblage distinct from the rest of the fishery.

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Statistical analyses of fisheries data often require consideration of the patchy distribution of aquatic organisms (e.g. Andrew and Pepperell, 1992). This is especially true with standard regression and ANOVA techniques because they rely on the assumptions of normality of residuals and homogeneous variances. Often, transformations of the response variable can be used to satisfy these assumptions (Underwood, 1981). However, in many instances suitable transformations cannot be found. In such cases, the use of standard regression and ANOVA techniques will result in gross violations of the model assumptions and affect the results of the analysis (Underwood, 1981). Where suitable transformations cannot be found, nonparametric techniques such as the Kruskal-Wallis one-way ANOVA or ANOVA on the ranked data have been used. As Underwood (1981) has noted, one of the implied assumptions of these methods, that of equal variances among treatments, is usually not satisfied when dealing with patchy data. A further problem with such techniques is that one cannot explore significant differences with the use of contrasts or multiple comparison tests, except with the Kruskal-Wallis one-way ANOVA. Therefore, when using these techniques, one is limited to the use of empirical methods to examine significant differences.

Studies on fisheries bycatch have used a variety of statistical methods. Andrew et al. (1995) used ANOVA with suitable transformations to evaluate the bycatch in an Australian stow-net fishery for school prawns, and Austin et al. (1994) used the Kruskal-Wallis one-way ANOVA to examine geographical differences in the bycatch of the Atlantic menhaden fishery. Hudson (1990), examining the shrimp and fish bycatch assemblages of the Canadian Eastern Arctic, used an intermediate linkage clustering algorithm to examine abundance patterns and species associations among different regions. More unique solutions have been pre-

sented by Richards et al. (1994), who proposed the use of a modified generalized logit model to carry out a categorical form of response surface analysis, allowing the estimation of transformation parameters on the explanatory variables along with other parameters. Perkins and Edwards (1996) have used mixture models, consisting of the negative binomial distribution with added zeros, as a solution to analyzing bycatch with many zero observations.

In this paper we use loglinear and logit models to examine patchy data with bycatch from the gulf menhaden, *Brevoortia patronus,* fishery. Menhaden bycatch can be classified into two groups: 1) bycatch that is pumped directly into the hold with the menhaden and that is termed "automatically retained bycatch"; and 2) all other bycatch that is termed "releasable bycatch." In this paper we analyze only releasable bycatch. With the exception of Christmas et al. (1960) and Condrey,[1] previous studies on menhaden bycatch have not taken releasable bycatch into account. Furthermore, all previous work has been qualitative in nature. Our examination of releasable bycatch, however, serves both as an analysis of patchy data with categorical techniques and as a quantitative description of a biologically important portion of the menhaden bycatch.

Species taken as bycatch may be caught because they are associated with the target species or simply because they were encountered on a random basis (Hall, 1996). An analysis of the structure of bycatch species assemblages associated with a fishery can provide valuable information for both management and ecological purposes. Hudson (1990), examining shrimp and fish bycatch assemblages in the Canadian Eastern Arctic, observed three associations that she proposed were related to the origin of the predominant water masses in the region. Harris and Poiner (1991) documented changes in the species composition of demersal fish fauna over a 20-year period in the Gulf of Carpentaria, Australia, and suggested that increases in the benthopelagic taxa over this period could be partially explained by discard of bycatch in the banana prawn fishery. Because little information on spatial and temporal associations for species assemblages of the menhaden fishery exists, we describe areal and temporal associations for these species, together with the fate of these species, as a first step in accruing such information. We have used correspondence analysis, a categorical form of ordination, to describe these association patterns.

[1] Condrey, R. E. 1994. Bycatch in the U.S. Gulf of Mexico menhaden fishery. Results of onboard sampling conducted in the 1992 fishing season. Coastal Fisheries Institute, Louisiana State Univ., Baton Rouge, LA. Final report for NA27F0007-01, 42 p. [Available through the NOAA library, Silver Springs, MD.]

The fishery

The U.S. Gulf of Mexico menhaden fishery has existed since the late 1800's (Nicholson, 1978) and is the largest fishery in tonnage in the northwestern Gulf of Mexico. Estimates of menhaden landings for the 1994 fishing season were approximately 0.7 million metric tons (t) (Leard et al., 1995). Although gulf menhaden is the primary clupeid sought, finescale menhaden, *B. gunteri*, yellowfin menhaden, *B. smithi*, and Atlantic thread herring, *Opisthonema oglinum,* are occasionally taken opportunistically (Leard et al., 1995).

Schools of menhaden are located visually by the senior crew aboard the fishing vessel or with the help of spotter planes. A purse seine, deployed from a pair of small (12.2-m) purse-seine boats, is used to encircle the school. Once the school is encircled, the bottom of the net is drawn up to hold the catch. The seine is then retrieved mechanically by each purse-seine boat until the fish are confined to a small section of the net. The catch is then pumped into the refrigerated hold of a larger (43 to 61 m) carrier vessel. The number of times the purse net is set each day depends on the availability and size of schools. Schools contain from 3 to 100 t of menhaden (Leard et al., 1995). Once the hold of a vessel is full, or a trip is otherwise complete, the menhaden are transported to one of the processing plants located from Moss Point, MS, to Cameron, LA. Although the fishing area extends from Apalachicola, FL, to Freeport, TX, more than 86% of the menhaden caught from 1990 to 1994 were taken off Louisiana (Leard et al., 1995).

Materials and methods

Loglinear and logit models

As reviewed in Agresti (1990) and Freeman (1987), loglinear and logit models are special cases of the generalized linear models introduced by Nelder and Wedderburn (1972). Agresti (1990) summarizes a generalized linear model as "a linear model for a transformed mean of a variable having a distribution in the natural exponential family."

Loglinear models describe association patterns among categorical variables. With this approach, cell counts in a contingency table are modeled in terms of association among the variables. Loglinear models may be viewed as analogous to correlation analysis where cell counts in a loglinear contingency table are treated as independent Poisson variables.

In a $I \times J$ table, where $N = IJ$ cells consisting of n multinomial samples, let n_k denote the count of the

k^{th} cell, and let $m_k = E(n_k)$ represent the expected value where $k = 1.....N$. The probabilities $\{\pi_{ij}\}$ for that multinomial distribution form the joint distribution of two categorical responses. These two responses are statistically independent when $\pi_{ij} = \pi_{i+}\,\pi_{+j}$ for all i and j.

If there is a dependence between the two variables, then all expected values of each cell (m_{ij}) are > 0. The loglinear model for this two-way table can be written as

$$\log m_{ij} = \mu + \lambda_i^x + \lambda_j^y + \lambda_{ij}^{xy},$$

where $\mu = \Sigma_i \Sigma_j \log m_{ij} / IJ$;
$\lambda_i^x = \Sigma_j \log m_{ij} / J - \mu$;
$\lambda_j^y = \Sigma_i \log m_{ij} / I - \mu$; and
$\lambda_{ij}^{xy} = \log m_{ij} - \lambda_i^x - \lambda_j^y + \mu$.

This model perfectly describes any set of positive expected frequencies and is referred to as the saturated model. The right-hand side of this equation resembles the formula for the cell-means ANOVA. The parameters $\{\lambda_i^x\}$ and $\{\lambda_j^y\}$ are deviations about a mean and $\Sigma_i \lambda_{ij}^{xy} = \Sigma_j \lambda_{ij}^{xy} = \Sigma_i \lambda_i^x = \Sigma_j \lambda_j^y = 0$. This model can also be described in the notation form as $[XY]$.

A saturated loglinear model always expresses a given table of categorical data perfectly. This model has the maximum achievable log likelihood because it is the most general model, with as many parameters as observations. However, it is possible that a simpler model may provide a fit as statistically good as that of the saturated model. How well this model fits is represented by the scaled deviance, a function of twice the difference in the log likelihoods of the saturated model and the simpler model. In addition to testing the fit of a model, one can use the deviance to diagnose lack of fit through residual analysis.

For example, consider a three-dimensional saturated model with variables X, Y, and Z. For this model $[XYZ]$, $\log m_{ijk} = \mu + \lambda_i^x + \lambda_j^y + \lambda_k^z + \lambda_{ij}^{xy} + \lambda_{ik}^{xz} + \lambda_{jk}^{yz} + \lambda_{ijk}^{xyz}$. When $\lambda_{ijk}^{xyz} = 0$, there is no three-factor interaction, and the association between two variables is identical at each level of the third variable and reduces to the loglinear model $[XY\,XZ\,YZ]$. Further, if $\lambda_{ijk}^{xyz} = 0$ and $\lambda_{jk}^{yz} = 0$, then for any given level of X, Y and Z are conditionally independent $[XY\,XZ]$. Similarly if $\lambda_{ijk}^{xyz} = 0$, $\lambda_{jk}^{yz} = 0$ and $\lambda_{ik}^{xz} = 0$, then Z is jointly independent of X and Y $[XY\,Z]$. Finally if $\lambda_{ijk}^{xyz} = 0$, $\lambda_{jk}^{yz} = 0$, $\lambda_{ik}^{xz} = 0$, and $\lambda_{ij}^{xy} = 0$, then X, Y, and Z are mutually independent $[X\,Y\,Z]$. With these criteria and beginning with a saturated model, we used a stepwise model selection procedure with deviance in the form of the G^2 test statistic to find a simpler model that fits as well as the saturated model. This simpler model would enable one to explore multidimensional tables to find simpler representations of the information contained therein.

Table 1

Hypothetical example used to explain odds ratios and conditional probabilities. $\pi_{j1|i}$ is the conditional probability of observing bycatch given a particular area. $\pi_{j2|i}$ is the conditional probability of observing no bycatch given a particular area.

	Bycatch			Conditional probabilities	
	Presence (j_1)	Absence (j_2)	Total sets	$\pi_{j1\|i}$	$\pi_{j2\|i}$
Area A (i_1)	4	6	10	0.40	0.60
Area B (i_2)	2	4	6	0.33	0.67
Total	6	10	16		

Another advantage of loglinear models is that when one of the variables can be modeled as a response, and the others as explanatory variables, certain loglinear models are equivalent to logit models with categorical explanatory variables. Such logit models enable us to study the problem of interest in a manner analogous to ANOVA.

Many categorical response variables have only two categories. The response can be classified either as a success or a failure. The Bernoulli distribution, which belongs to the natural exponential family, forms the basis of modeling the logit model. For such a dichotomous variable, the probability of observing response 0 can be defined as $P(Y=0) = \pi$, and the probability of observing response 1, as $P(Y=1) = 1 - \pi$. The link function for this model, $\log \pi_i / (1-\pi_i)$, known as the logit, is equivalent to the log odds.

Consider the following example, where we examine the presence or absence of bycatch in two areas. In this example (Table 1), the 2×2 table has rows i_1*(area 1)*, and i_2 *(area 2)* and columns j_1 *(presence of bycatch)* and j_2 *(absence of bycatch)*. The counts in the cells of the table are the number of units of effort (individual sets) observed in each category.

In this case, the odds, Ω_{i1}, of observing j_1 *(presence of bycatch)* given you are in category i_1 *(area 1)* is computed as the ratio of the conditional probabilities of observing a set with bycatch to that of observing a set with no bycatch in area 1:

$$\left\{\pi_{j1|i1}/\pi_{j2|i1}\right\} \text{ is } 0.4/0.6 = 0.67.$$

Similarly, the odds, Ω_{i2}, of observing j_1*(presence of bycatch)* given you are in category i_2 *(area 2)* is computed as the ratio of the conditional probabilities of

observing a set with bycatch to that of observing a set with no bycatch in area 2:

$$\left\{\pi_{j1|i2}/\pi_{j2|i2}\right\} \text{ is } 0.33/0.67 = 0.5.$$

The odds ratio, θ, is computed as

$$\Omega_{i1}/\Omega_{i2} \text{ is } 0.67/0.5 = 1.34.$$

Thus, the odds of observing response j_1 *(presence of bycatch)* is 1.34 times more likely for row i_1 *(area 1)* than for row i_2 *(area 2)*. An odds ratio of 1 indicates that you are equally likely to observe response j_1*(presence of bycatch)* for row i_1 *(area 1)* and row i_2 *(area 2)* and thus indicates independence between the rows and columns of the table.

The logit model has two forms. One form occurs where the explanatory variables are continuous and is the logistic regression model. The second occurs where the explanatory variables are categorical. The logistic regression model is analogous to a regression model, whereas the second type is analogous to an ANOVA model.

For the previous example, a model with a single categorical explanatory factor (area), the logit form of the model is

$$\log(\pi_{j1|i}/\pi_{j2|i}) = \alpha + \beta_i^{Area},$$

where α = the mean of the logits; and
β_i^{Area} = the deviation from the mean for row i.

β_i describes the effects of the factor on the response. For this model the higher β_i becomes, the higher the logit in row i, and the higher the value of $\pi_{j1|i.}$ The constraints on this model are $\Sigma\ \beta_i = 0$. In this case the right-hand side of the equation resembles the cell-means model of a one-way ANOVA. This logit model would be equivalent to $\log(m_{ij1}) - \log(m_{ij2}) = 2\lambda_i^{Area} + 2\lambda_{j1}^{Bycatch} + 2\lambda_{ij1}^{AreaBycatch}$ in loglinear form.

Bycatch sampling and data set description

Bycatch from the gulf menhaden fishery was sampled April through October 1995 by two to three onboard samplers on a total of twenty-seven week-long trips aboard vessels operating from menhaden processing plants in the U.S. Gulf of Mexico. To maximize coverage of the Gulf, samplers boarded vessels from ports in the western, central, and eastern regions in a given week as often as possible. During each sampling trip, all sets made by the vessel were alternatively sampled, either for releasable bycatch or automatically retained bycatch. For all sets sampled, the presence of dolphins in the vicinity was also noted by the observers. In addition, the boat captains visually estimated catch in standard menhaden (1,000 standard menhaden [~305 kg]) and recorded the latitude and longitude of a set location. The location was used to identify in which National Marine Fisheries Service (NMFS) statistical zone (Fig. 1) the set was made (after Kutkuhn, 1962).

To collect releasable bycatch data, samplers observed the purse seine from the time it was brought alongside the carrier ship and throughout the pumping procedure, until the net was emptied and cleaned. During this time, the species, number, and fate of the releasable bycatch were recorded. The seven categories of bycatch fate were as follows: gilled in the net (gilled); kept by the crew for consumption (kept); released with no apparent harm (released healthy); released seriously injured or dead (released dead); released after being bruised or after being kept in the set for a long time (released disoriented); collected by the crew from the net or deck and put into the hold (caught and put in hold); and observed in the net but fate unknown (unknown).

Statistical analysis

Preliminary analysis For the variables bycatch number, bycatch percentage, and estimated catch, we calculated a series of commonly used statistical descriptors, namely the mean, standard deviation, 95% confidence intervals, median, skewness, and kurtosis. In addition, we also calculated the winsorized mean and its standard deviation.

We initially attempted to examine spatial and temporal patterns in the bycatch with a two-way ANOVA model. For the analysis, data were classified into season (S) consisting of three groups: 1) spring (April through June), 2) summer (July through August), and 3) fall (September through October). Adjacent NMFS zones (Fig. 1) were combined to form four area (A) groups: 11–12, 13–14, 15–16, and 17–18.

Bycatch patterns were examined with two response variables: 1) bycatch numbers; and 2) bycatch percentage ([bycatch number/total catch] × 100). For each of these two response variables, spatial and temporal patterns were examined by using the ANOVA model with season, area, and their interaction term as independent variables. Because we anticipated that neither model would satisfy the model assumptions of normality of residuals and homogeneous variances, we also examined the models by using the log and square-root transformations for both response variables. In addition we also used 2 arcsin $\sqrt{}$ (bycatch/menhaden catch) suggested by Neter et al. (1990) for transformation of proportions. All seven

models were examined to determine if model assumptions were met.

Spatial and temporal patterns in bycatch For our analysis using loglinear and logit models with categorical explanatory variables, we used a four-way contingency table with a unit of effort (the set) as the count. Our main interest was 1) to examine the spatial and temporal patterns in bycatch and 2) to determine if the presence of dolphins in the vicinity when the set was made might be an indicator of bycatch patterns.

Exploratory analysis with loglinear and logit models To examine bycatch as a response of interest with categorical models, a new dichotomous categorical variable, bycatch, based on the median bycatch percentage, was created. Each set was classified either as high bycatch if the bycatch rate of the set was greater than the median value of all sets or as low bycatch if the bycatch rate of the set was less than or equal to the median bycatch of all the sets. We used the median rate because it is a robust measure of central tendency. In deciding on possible criteria for defining this variable, more extreme conditions, such as bycatch rates greater than the 75th percentile, were considered. However, by choosing more extreme values, we increased the number of sparse cells and thus affected the validity of the G^2 test statistic.

In analyzing contingency tables, it is necessary that the number of cell counts with zero frequencies be low (a minimum expected value of 1 is satisfactory as long as <20% of cells have counts of 5 or less) for the test statistic to be valid (Agresti, 1990). To reduce the number of cells with zero frequencies, months and zones were combined, generating two new variables, season and area, corresponding to those used in the ANOVA. The presence of dolphins was used as a dichotomous variable, dolphins *(D)*.

To identify the most appropriate and simplest loglinear model for the data using the variables season, area, bycatch, and dolphins, we employed a stepwise backward solution procedure commencing with the saturated loglinear model (Agresti, 1990). Here the saturated model

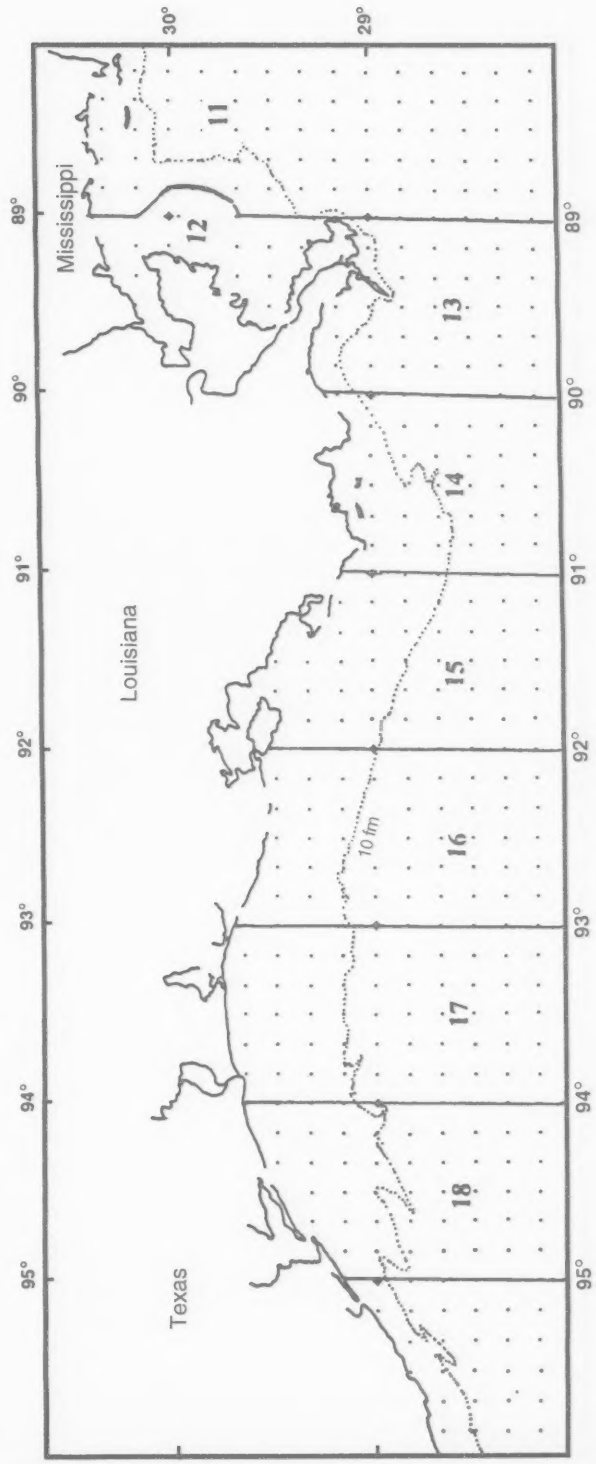

Figure 1
Map encompassing the extent of the U.S. gulf menhaden fishery from the Texas to Alabama coasts. The eight fishing zones numbered 11–18 are from NMFS (after Kutkuhn, 1962).

is denoted as [*SABD*] were *S* stands for season, *A* for area, *B* for bycatch, and *D* for dolphins, and the model includes all possible interactions up to and including the four-way interaction. Because the saturated model would naturally provide the best fit, we were interested in determining if a simpler model could be found that would also satisfy the criteria of a logit model with bycatch as the response variable. The standardized residuals of the resulting model were then examined to ensure that lack of fit was not a problem.

Contrasts We anticipated that we would have significant interaction terms in our analyses that would require detailed examination of interactions. For the logit form of the selected model, we constructed a series of contrasts that might help to explain the nature of these potential interactions. The contrasts of interest had two general forms:

1 Given a specific area, are the odds of observing a set with high bycatch the same between any two different seasons. This results in three unique contrasts for each area (spring vs. summer, spring vs. fall, summer vs. fall) and a total of 12 contrasts.

Let F_{ij} be the logit of high bycatch for season i and area j and let F_{hj} be the logit of high bycatch for season h and area j.

The hypotheses being tested were

$$H_0: F_{ij} - F_{hj} = 0,$$

where $F_{ij} = \alpha + \beta_i^S + \beta_j^A + \beta_{ij}^{SA}$;
$F_{hj} = \alpha + \beta_h^S + \beta_j^A + \beta_{hj}^{SA}$; and
h and i = spring, summer, and fall, such that $h \neq i$ for each j, and j = area 11–12, area 13–14, area 15–16, and area 17–18.

2 Given a specific season, are the odds of observing a set with high bycatch the same between any two different areas. This results in six unique contrasts for a given season and a total of 18 contrasts (11–12 vs. 13–14, 11–12 vs. 15–16, 11–12 vs. 17–18, ... ,15–16 vs. 17–18).

Let F_{ij} be the logit of high bycatch for season i and area j and let F_{ik} be the logit of high bycatch for season i and area k.

The hypotheses being tested were

$$H_0: F_{ij} - F_{ik} = 0,$$

where $F_{ij} = \alpha + \beta_i^S + \beta_j^A + \beta_{ij}^{SA}$;
$F_{ik} = \alpha + \beta_i^S + \beta_k^A + \beta_{ik}^{SA}$; and
j and k = area 11–12, area 13–14, area 15–16, and area 17–18, such that $j \neq k$ for each i, where i = spring, summer, and fall.

Because 30 contrasts were performed, the type-I error level of 0.10 was adjusted by using the Bonferroni technique, and only *P*-values less than 0.0033 were considered significant. The estimated odds ratios for the conditions associated with the hypotheses were calculated from the parameter estimates given by the analysis.

Bycatch species associations To examine the association between species and fates of the releasable bycatch, we used correspondence analysis on a species-by-fate table for all seasons and areas combined. Area and species associations of the releasable bycatch were also examined for each of the three seasons with correspondence analysis on species-by-area tables.

For all correspondence analyses we defined two groups of species. The first group, consisting of those species that were common in terms of number and occurrence, was used in the main table. Releasable bycatch species falling into this group had a minimum of 230 individuals and were found in at least 30% of the sets. The second group of species consisted of releasable bycatch that were less common; these were species for which a minimum of 30 individuals were observed, which occurred in at least 4% of the sets, and which did not meet our criteria for well represented species. These species were included as supplementary variables in our analysis (Greenacre, 1984). Supplementary variables are represented as points in the joint row and column space but are not used in determining the locations of the active rows and columns of the table. Species included in the main and supplementary table accounted for 97% of the total number of organisms observed during the study period. Species that did not meet these criteria were not used in the analyses.

Results

Preliminary analysis

A total of 15,579 bycatch organisms representing 62 species or species groups were observed as releasable bycatch in 257 sets. The estimated catch of standard menhaden per set ranged from 5,000 to 500,000 with a median, mean, and standard deviation of 50,000, 67,000, and 61,000 respectively. Skewness and kurtosis values of 2.5 and 10.7 indicated that the distribution of the estimated menhaden catch was positively skewed (Fig. 2).

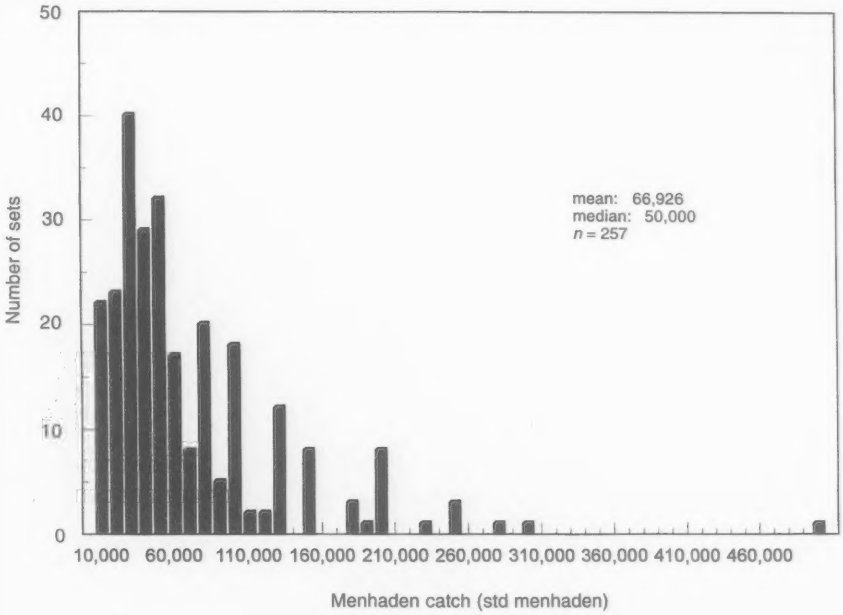

Figure 2

Distribution of menhaden catch sampled during the 1995 gulf menhaden fishing season. std = standard (1,000 standard menhaden ~ 305 kg).

The number of bycatch observed in each set ranged from 0 to 1,600 organisms, with a median, mean, and standard deviation of 15, 61, and 153 respectively. The winsorized mean and its standard deviation values were 53 and 6.9 respectively. The 95% confidence interval of the mean was between 41.8 and 79.3. The distribution of bycatch organisms was strongly positively skewed (5.9) and peaked sharply with a Kurtosis value of 47.2 (Fig. 3).

The bycatch percentage ranged from 0% to 4% with a median, mean, and standard deviation of 0.033%, 0.168%, and 0.48 respectively. The winsorized mean bycatch percentage and its standard deviation were 0.14% and 0.02, respectively. The 95% confidence interval of the mean was between 0.11% and 0.22%. The distribution of the bycatch percentage was also found to be positively skewed and strongly peaked, with skewness and kurtosis values of 5.4 and 32.7 respectively (Fig. 4).

Analysis of variance with bycatch, bycatch percentage, and their respective transformations, together with the arcsine transformation, did not meet model assumptions. In all cases the modified Levene's test indicated that the variances were nonhomogeneous, and both the residual plots and Shapiro-Wilk test indicated that the assumption of normality of residuals were not met. For example, for the response log (bycatch percentage + 1), the residuals of the model were not normally distributed (Shapiro-Wilk W=0.678, $P<W$=0.0001), and the residual plot indicated nonhomogenous variances. Furthermore, a modified Levine's test indicated that the variances were nonhomogeneous (F=6.21, df=11, df-error=245, $P>F$=0.0001). These characteristics suggest that the model assumptions were grossly violated and that ANOVA may not be an appropriate form of analysis in this case.

Spatial and temporal patterns in bycatch

Exploratory analysis using loglinear models With the backward selection procedure, loglinear models [SAB SAD DB] and [SAB SAD] (as defined in Table 2) satisfied the criteria for a logit model and had good fit (Table 2). The simplest of these models, [SAB SAD], was selected; this loglinear model corresponds to the logit model with categorical explanatory variables of the form

$$\log\frac{\pi_{highlik}}{\pi_{lowlik}} = \alpha + \beta_i^A + \beta_k^S + \beta_{ik}^{AS}, \qquad (1)$$

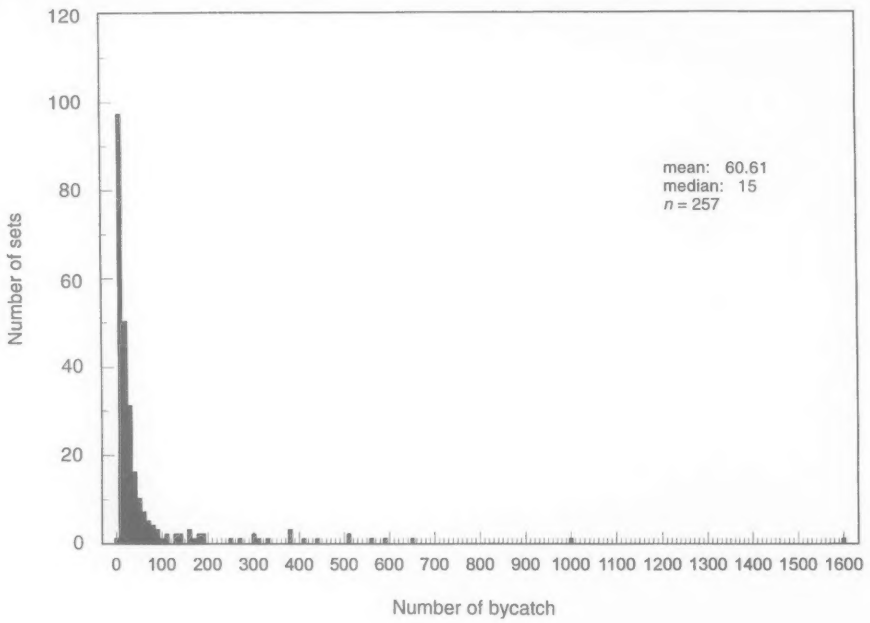

Figure 3

Distribution of bycatch sampled during the 1995 gulf menhaden fishing season.

Table 2

Summary statistics of loglinear models examined through the stepwise selection procedure. Models with fits as good as the saturated model are marked ns. (A=area, B=bycatch, D=dolphins, S=season). Models are presented hierarchically from most complex to simplest.

Loglinear model	df	G^2	P-value
Model without the four-way interaction term			
ADB SDB SAB SAD	6	11.64	0.0706
Selected models with 3 three-way interaction terms			
ADB SDB SAB	12	26.58	0.0089
ADB SDB SAD	12	27.62	0.0063
SDB SAB SAD^{ns}	9	13.41	0.1449
SAB SAD ADB	14	27.90	0.0147
Selected models with 2 three-way and 1 two-way interaction terms			
SDB SAB DA	15	29.38	0.0144
SAB SAD DB^{ns}	11	15.65	0.1547
Selected models with 2 three-way interaction terms			
SAB SAD^{ns}	12	17.82	0.1213
SDB SAB	18	45.83	0.0003
Selected models with 1 three-way and 2 two-way interaction terms			
SAB SD AD	18	34.89	0.0097
SAD SB AB	18	34.30	0.0116

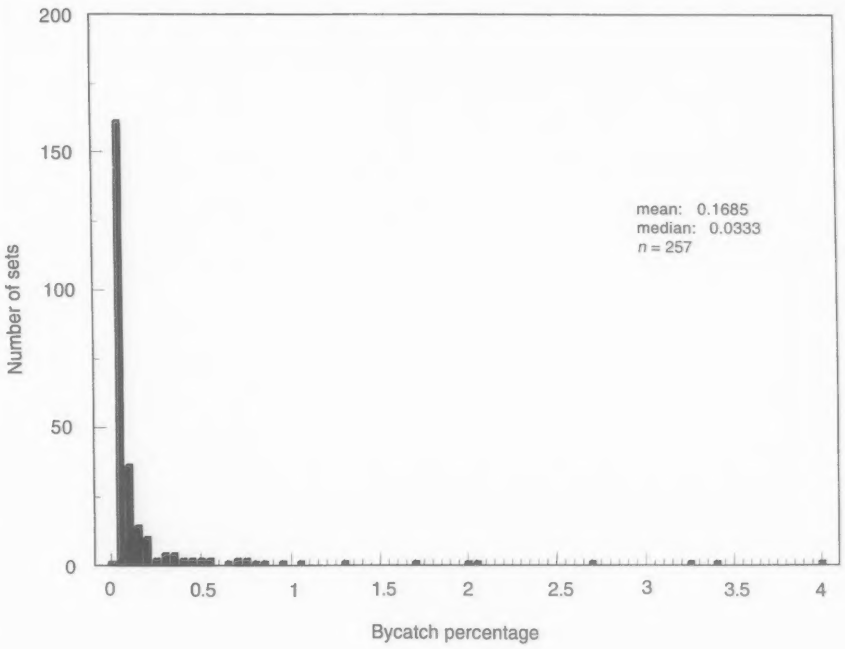

Figure 4

Distribution of the bycatch percentage in fishing sets sampled during the 1995 gulf menhaden fishing season.

where $\pi_{high|ik}$ = the probability of observing a set with high bycatch given area i and season k; and

$\pi_{low|ik}$ = the probability of observing a set with low bycatch given area i and season k.

This model, in loglinear and logit forms, had a G^2=17.82, with 12 df and a P-value=0.1213. Examination of the standardized residuals of the logit form revealed that none of the residuals had an absolute value greater than 1.45 and thus showed no evidence of lack of fit.

For the logit model, there was a significant interaction between season and area (Wald chi-square (χ^2)=14.65, df=6, P=0.0232). This interaction is reflected in the plot of probabilities of high (greater than 0.033%) bycatch for the area-season combinations (Fig. 5).

Contrasts The contrasts of the odds of high bycatch between seasons for a given area indicate that the hypothesis of spring and summer seasons being the same for all four areas could not be rejected. Wald χ^2 values are presented in Table 3. The contrasts of the spring and fall seasons suggest that the only signifi-

Table 3

Estimated odds ratios and Wald chi-square (χ^2) values of contrasts of observing high bycatch between seasons, given a set was made in a certain area. For example, the odds of observing high bycatch is 11.761 times greater during the spring season than during the fall season for area 11–12. * indicates a ratio significantly different from 1. Wald χ^2 values are in parenthesis. For all contrasts, Wald χ^2 df = 1.

Season	Area	Spring		Fall	
Fall	11–12	11.761*	(10.03)		
Summer	11–12	1.142	(0.05)	0.097*	(9.25)
Fall	13–14	4.444	(2.24)		
Summer	13–14	0.555	(0.19)	0.125	(2.41)
Fall	15–16	0.699	(0.48)		
Summer	15–16	0.414	(4.29)	0.592	(0.97)
Fall	17–18	0.312	(2.11)		
Summer	17–18	0.218	(2.47)	0.899	(0.02)

cant differences between these two seasons existed for area 11–12 (Wald χ^2=10.03, df=1, $P>\chi^2$=0.0015). When the summer and fall seasons were contrasted, a significant difference between seasons was observed only for area 11–12 (Wald χ^2=9.25, df=1, $P>\chi^2$=0.0024).

For contrasts of the odds of high bycatch between areas for a given season, significant differences between areas 11–12 and 17–18 in the spring season were observed (Wald χ^2=9.29, df=1, $P>\chi^2$=0.0023). All other contrasts between areas for the spring, summer, and fall seasons were not significant. Wald χ^2 values for these contrasts are presented in Table 4.

The estimated odds ratios for the conditions associated with the hypotheses are also given in Tables 3 and 4. Only estimated odds ratios of contrasts for the rejected hypotheses of no difference are examined in detail.

If a fishing boat was in area 11–12, the odds of observing a set with high bycatch are about 11.8 times higher if a boat was fishing in the spring rather than the fall. Also, if a fishing boat was in area 11–12, the odds of observing a set with high bycatch are about 0.1 times (or approximately 10.3 times lower) in the fall than in the summer. It appears that for area 11–12, the odds of observing a set with high bycatch in the fall are significantly lower than in the spring or summer.

The third significant contrast indicated that for a vessel fishing in the spring, the odds of observing a set with high bycatch are about 10.8 times higher in area 11–12 than in area 17–18.

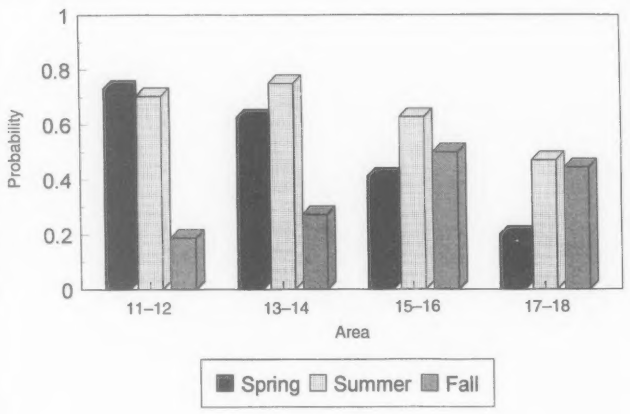

Figure 5

Probabilities of observing a set with high bycatch (> 0.033%) for the season-area combinations.

Table 4

Estimated odds ratios and Wald chi-square (χ^2) values for contrasts (in parentheses) for observing high bycatch between areas, given a set was made in a certain season. For example, the odds of observing high bycatch are 1.628 times greater in area 11–12 than in area 13–14. * indicates a ratio significantly different from 1. Wald χ^2 values are in parenthesis. For all contrasts, χ^2 df=1.

		Area		
Season	Area	11–12	13–14	15–16
Spring				
	13–14	1.628 (0.33)		
	15–16	3.877 (6.64)	2.380 (1.23)	
	17–18	10.857* (9.29)	6.666 (3.79)	2.799 (2.13)
Summer				
	13–14	0.791 (0.04)		
	15–16	1.407 (0.42)	1.777 (0.23)	
	17–18	2.671 (2.33)	3.374 (0.94)	1.898 (1.22)
Fall				
	13–14	0.615 (0.27)		
	15–16	0.230 (3.63)	0.375 (1.50)	
	17–18	0.288 (2.43)	0.468 (0.84)	1.250 (0.12)

Refining the final model We were interested, on the basis of our contrasts, in determining if a model with simpler dichotomous classes for areas and seasons would provide as good a statistical fit as this "full model" (Eq. 1). We compared three potential models that had one or both of these variables with reduced classes against the full model (Table 5). For these models we classified area into two groups: 1) east of the Mississippi River; and 2) west of the Mississippi River. Season was also classified into two groups; 1) early—sets sampled April through August; and 2) late—sets sampled September through October.

All three reduced models provided a fit as good as that of our full model (Table 5); therefore we chose the model that had reduced classes for season and area because it was the simplest. Four contrasts of interest were examined:

1 Test for seasonal differences in the odds of observing a set with high bycatch given the set was sampled east of the Mississippi River;

2 Test for seasonal differences in the odds of observing a set with high bycatch given the set was sampled west of the Mississippi River;
3 Test for area differences in the odds of observing a set with high bycatch given the set was sampled in the early season; and
4 Test for area differences in the odds of observing a set with high bycatch given the set was sampled in the late season.

The contrasts were written similarly to those for the "full model." For the four contrasts, we used an α level of 0.025 as significant.

Of the four contrasts, two were significant. The first indicated that in areas east of the river, the odds of observing a set with high bycatch was significantly different between sets sampled in the early season and sets sampled in the late season (Wald χ^2=11.41, df=1, $P>\chi^2$= 0.0007). The odds of observing a set with high bycatch east of the river in the early season was 11 times greater than the odds of observing a set with high bycatch in the late season. The second significant contrast indicated that for sets sampled in the early season, the odds of observing a set with high bycatch east of the river was significantly different from the odds of observing a set with high bycatch west of the river (Wald χ^2=7.99, df=1, $P>\chi^2$=0.0047). In the early season, the odds of observing a set with high bycatch east of the river was 2.7 times greater than observing a set with high bycatch west of the river during the same period.

Table 5

Comparison of reduced logit models with the full model. Diff = difference between full model and reduced model.

	Likelihood ratio statistics			Model comparisons		
	df	G^2	$P > G^2$	Diff (df)	Diff (G^2)	*P*-Value
Full model Season= Apr–Jun, Jul–Aug, Sep–Oct Area = 11–12, 13–14, 15–16, 17–18	12	17.82	0.1213			
Reduced model I Season=spring, summer, fall Area = 11–12, 13–18	6	9.76	0.1352	6	8.06	0.237
Reduced model II Season=Apr–Aug, Sep–Oct Area = 11–12, 13–14, 15–16, 17–18	8	9.99	0.2659	4	7.83	0.098
Reduced model III Season= Apr–Aug, Sep–Oct Area = 11–12, 13–18	4	7.54	0.1100	8	10.28	0.246

Bycatch species associations

Of the 62 species groups observed, 20 occurred in two or fewer sets. The most frequently occurring species were Atlantic cutlassfish, *Trichiurus lepturus* (44% of sets), Atlantic croaker, *Micropogonias undulatus* (38% of sets), Spanish mackerel, *Scomberomorus maculatus* (36% of sets), sand seatrout, *Cynoscion arenarius* (35% of sets), and gafftopsail catfish, *Bagre marinus* (34% of sets). In terms of total abundance (Table 6), Atlantic croaker, sand seatrout, and Atlantic bumper, *Chloroscombrus chrysurus*, accounted for 71% of the total releasable bycatch.

Species included in the main table were Atlantic croaker, sand seatrout, crevalle jack, *Caranx hippos*, gafftopsail catfish, Spanish mackerel, and Atlantic cutlassfish (Table 6). Species included as supplementary variables were striped mullet *Mugil cephalus*, unidentified requiem sharks, gulf butterfish, *Peprilus burti*, cownose ray, *Rhinoptera bonasus*, spotted seatrout, *Cynoscion nebulosus*, Atlantic bumper, blacktip shark, *Carcharhinus limbatus*, red drum, *Sciaenops ocellatus*, unidentified penaeid shrimp, hardhead catfish, *Arius felis*, brown shrimp, *Panaeus aztecus*, cabbage head jellyfish, *Stomolophus meleagris*, bull shark, *Carcharhinus leucas*, and unidentified tonguefish (Soleidae) (Table 6).

The fate of releasable bycatch Correspondence analysis on the fate-by-species table for the entire fishing season indicated that the first two axes explained 97% of the total inertia (conceptually similar to variance) and offered a good representation of the fate-species associations. From the two-dimensional plot (Fig. 6) we discerned three major and one minor groupings.

Species primarily associated with being released dead or disoriented were unidentified requiem sharks, red drum, crevalle jack, and bull sharks. Species secondarily associated with being released dead or disoriented were cownose rays and blacktip sharks. These last two species were primarily associated with being released healthy and appeared to form their own minor grouping.

Table 6

Species used in correspondence analyses. (M) signifies species used in main table and (S) in supplementary table (see "Materials and methods" section. Areas (11–12, 13–14, etc. are shown under each season. Counts are number of organisms observed. Unid. = unidentified.

	Spring				Summer				Fall				
	11–12	13–14	15–16	17–18	11–12	13–14	15–16	17–18	11–12	13–14	15–16	17–18	Total
Atlantic croaker (M)	132	20	50	1	554	1,604	1,732	212	40	97	51	612	5,105
sand seatrout (M)	104	26	17	0	813	1,500	572	2	91	91	197	53	3,466
gafftopsail catfish (M)	255	70	72	24	161	0	96	48	8	28	33	1	796
Atlantic cutlassfish (M)	41	28	209	22	5	1	53	55	7	0	13	36	470
crevalle jack (M)	71	12	133	17	5	0	31	9	22	41	8	0	349
Spanish mackerel (M)	22	11	34	33	29	0	56	33	0	7	6	10	241
Atlantic bumper (S)	0	0	0	0	0	0	2,166	330	0	0	1	0	2,497
striped mullet (S)	344	31	0	0	511	0	0	0	0	9	0	0	895
red drum (S)	21	0	34	0	23	0	24	6	0	12	9	116	245
hardhead catfish (S)	36	5	3	0	100	3	38	3	12	1	3	2	206
tonguefish spp. (S)	0	0	2	0	0	0	1	0	0	0	200	1	204
blacktip shark (S)	37	0	54	1	20	0	19	52	0	0	0	1	184
cownose ray (S)	27	2	26	0	3	0	4	7	0	0	1	0	70
brown shrimp (S)	0	0	1	2	0	0	39	0	0	0	10	13	65
cabbbagehead jellyfish (S)	0	0	5	12	0	0	33	0	1	0	4	6	61
unid. requiem sharks (S)	0	0	23	2	3	0	16	0	0	6	1	6	57
spotted seatrout (S)	2	8	0	0	31	0	0	0	0	0	0	0	41
gulf butterfish (S)	2	0	3	0	0	0	6	3	0	0	0	26	40
bull shark (S)	5	0	0	0	31	0	2	0	0	0	0	1	39
unid. penaeid shrimp (S)	0	0	1	9	5	0	0	0	1	0	0	16	32
Others (not used in CA)	80	5	86	11	147	5	56	24	13	8	72	9	516
Column Total	1,179	218	753	134	2,441	3,113	4,944	784	195	300	609	909	15,579

The second group, species primarily associated with being gilled, were Atlantic croaker, sand seatrout, and unidentified tonguefish. Other species that were associated with being gilled were unidentified penaeid shrimp, Atlantic cutlassfish, gulf butterfish, and Atlantic bumper. These four species were also associated with the third group, species kept by the crew, and those whose fate was unknown. Other species associated with this third group were hardhead catfish, brown shrimp, Spanish mackerel, gafftopsail catfish, striped mullet, and the cabbage head jellyfish.

Temporal and spatial patterns of bycatch species

Spring Correspondence analysis of area by species for spring indicated that the first two axes explained 97% of the inertia and offered a good representation of species-area associations. From the two-dimensional plot (Fig. 7), we discerned three major groupings. The first axis separates the eastern areas of the fishery (zone groups 11–12 and 13–14) from the western areas (zone groups 15–16 and 17–18). The second axis also separates zone group 15–16 from zone group 17–18.

The eastern areas are associated with Atlantic croaker, gafftopsail catfish, sand seatrout, hardhead catfish, bull shark, striped mullet, and spotted seatrout.

Zone group 15–16 is primarily associated with unidentified tonguefish, red drum, crevalle jacks, blacktip shark, unidentified requiem sharks, gulf butterfish, and Atlantic cutlassfish. Zone group 17–18 was associated with Spanish mackerel, brown shrimp, cabbage head jellyfish, and unidentified shrimp.

Summer For the summer, correspondence analysis indicated that the two axes accounted for 94% of total inertia. As in spring, three major species area groupings were observed (Fig. 8). Notable differences in these grouping were that zone group 15–16 appeared to be closer to the eastern groups (13–14 and 11–12). Furthermore, group 13–14 was separated further from zone group 11–12.

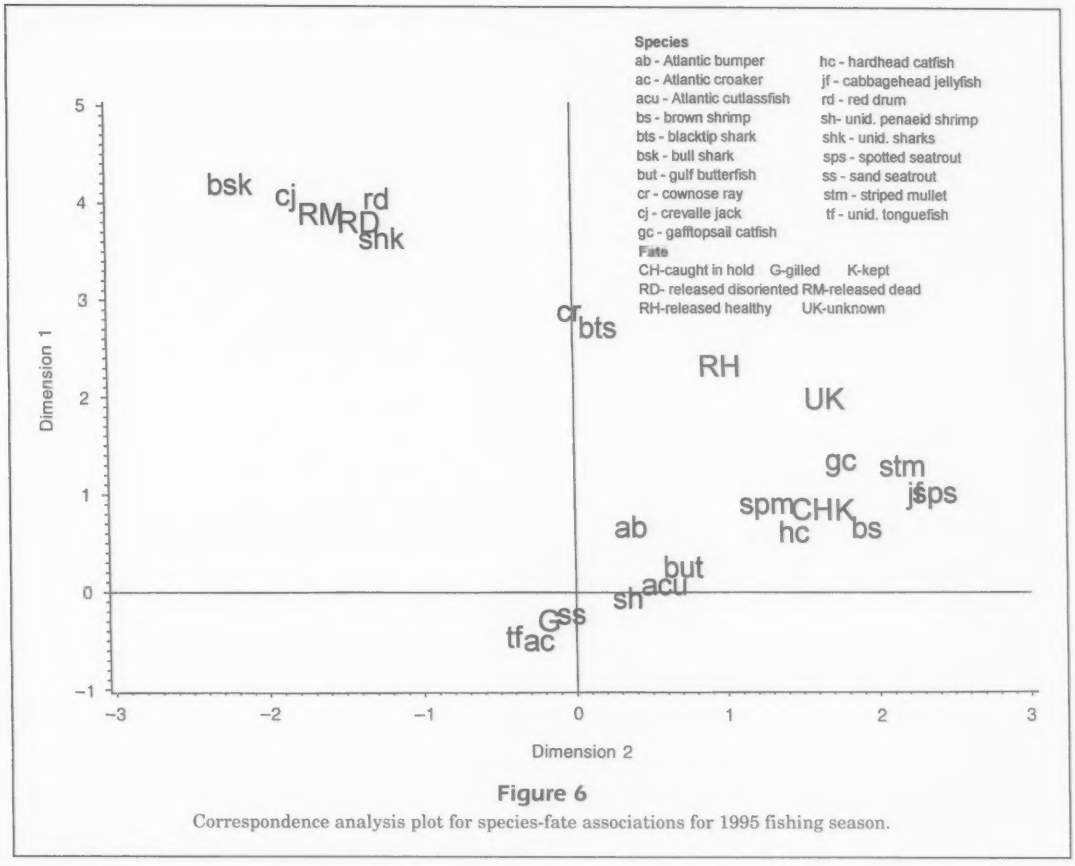

Figure 6

Correspondence analysis plot for species-fate associations for 1995 fishing season.

Zone groups 11–12 and 13–14 were primarily associated with sand seatrout and, to a lesser extent, Atlantic croaker. In addition, zone group 11–12 was also associated with bull shark, striped mullet, spotted seatrout, unidentified shrimp, and hardhead catfish.

Zone group 15–16 was also associated with Atlantic croaker. Other species associated with this area were cabbage head jellyfish, brown shrimp, unidentified tonguefish, Atlantic bumper, unidentified requiem sharks, gulf butterfish, and crevalle jack. Zone group 17–18 was associated with Spanish mackerel, Atlantic cutlassfish, cownose ray, blacktip shark, red drum, and gafftopsail catfish. Secondarily associated species with this area were gulf butterfish and crevalle jack.

Fall The first two axes of the fall analysis explained 97% of the total inertia, once again presenting a good fit of the table. By fall, two major groupings were observed (Fig. 9). Areas from zone group 11–12 to 15–16 formed one group and were separated from the most westerly zone group 17–18.

Zone group 17–18 was primarily associated with Atlantic croaker, red drum, bull shark, blacktip shark, gulf butterfish, unidentified shrimp, and, to a lesser extent, cabbage head jellyfish, brown shrimp, spotted seatrout, Spanish mackerel, and unidentified requiem sharks.

Zone groups 11–12 to 15–16 were associated with hardhead catfish, gafftopsail catfish, sand seatrout, and, to a lesser degree, Spanish mackerel. In addition zone group 13–14 was also associated with crevalle jack and striped mullet and zone group 15–16 with cownose ray, unidentified tonguefish, and Atlantic bumper.

Discussion

Bycatch studies of the menhaden industry were conducted in 1894 on the Atlantic menhaden, *Brevoortia tyrannus*, fishery (Christmas et al., 1960) and in 1948 in the U.S. Gulf of Mexico (Miles and Simmons, 1950). Automatically retained bycatch percentage estimates

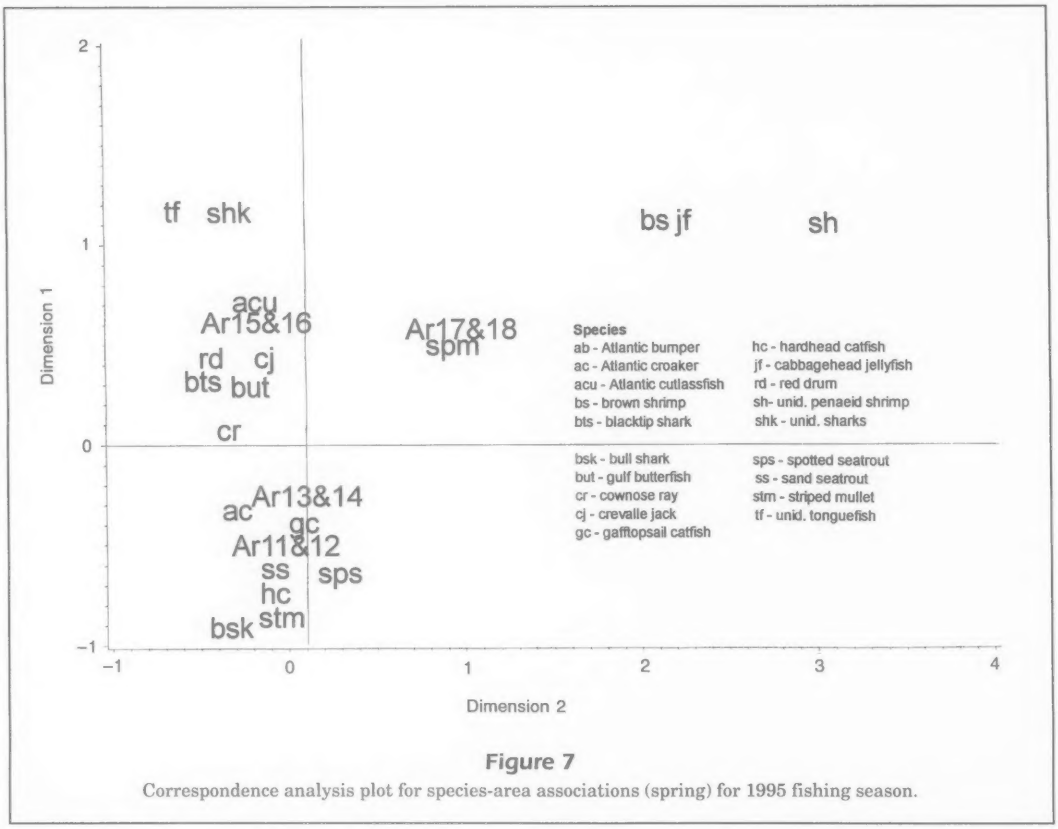

Figure 7

Correspondence analysis plot for species-area associations (spring) for 1995 fishing season.

have ranged from 0.05% (Dunham, 1972) to 3.90% (Christmas et al., 1960) by number, and 1.0% (Condrey[1]) to 2.80% (Christmas et al., 1960) by weight. However, these values are based on bycatch retained in the fish hold. No estimates of the releasable bycatch are available. Based on our analysis, releasable bycatch estimates for the U.S. Gulf of Mexico menhaden fishery range from 0.033% (median) to 0.17% (mean) and reflect the strong positively skewed distribution of the bycatch. Values based on the winsorized mean are intermediate to those of the mean and median and are associated with a lower standard deviation than that for the mean.

As a result of the patchy distribution of menhaden bycatch, examination of the relationship of bycatch to other factors is made more complex. Even after the transformation of our data, gross violations of the ANOVA model assumptions made it an unsatisfactory technique. Because we could not find a suitable transformation, our solution to examining such data would be to convert the variable of interest into a categorical variable and to use categorical techniques in analyzing the data. In our case, the use of loglinear models to identify statistically important interactions was found to be a useful tool in exploring such data. This solution can be considered to fall between studies that can use ANOVA techniques (e.g. Andrew et al., 1995) and those based on the modified negative binomial model as used by Perkins and Edwards (1996).

Legendre (1987) noted that the responses of living organisms to environmental change is nonlinear and in instances nonmonotonic. As loglinear models are insensitive to the shape of the relationship among the variables, Legendre (1987) noted that they are well suited for examining nonmonotically related variables. A further advantage of this type of analysis is that because biological variables respond to interacting environmental variables, they can be used to examine such relationships in detail. By using loglinear models we can include a set of potential interactions in our saturated model, and through a stepwise selection procedure, find those interactions that are statistically important. In our study, bycatch was the issue of interest and the variable that we treated as a response. In effect, we were trying to

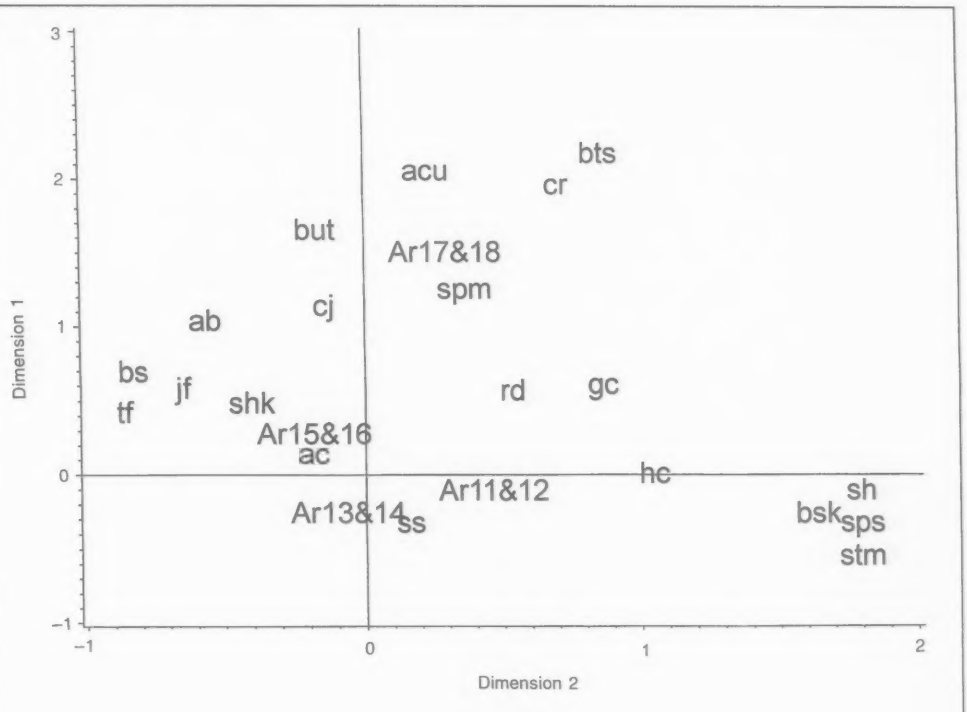

Figure 8

Correspondence analysis plot for species-area associations (summer) for 1995 fishing season.

find factors that could explain the bycatch, and we used loglinear models to find a suitable model that was associated with occurrences of bycatch greater than the median level for the fishery.

By using both loglinear models and logit models with categorical explanatory variables, we have used the loglinear model for model selection and the logit model for a detailed examination of the model of our choice in a manner analogous to ANOVA.

With the stepwise selection procedure, [SAB SAD] was found to be the most suitable loglinear model. We had hypothesized that the presence of dolphins in the fishing area could indicate the presence of high bycatch. Had this been true, the presence of dolphins in the vicinity could have been used by fishermen to avoid setting nets in certain areas. However, such a relation between dolphins and bycatch was found not to exist.

At first glance the issue of bycatch in Gulf of Mexico menhaden fishery may seem to be negligible, given the low bycatch percentage. However the fishery had the second highest annual U.S. commercial landings of 472,000 t in 1995 (U.S. Dep. Commerce, 1996). Further, given the strong positively skewed distribution of releasable bycatch, a small percentage of the total fishing effort would account for much of the take. By structuring our analysis around bycatch rates that were greater than the median, we have attempted to identify the potential "hot spots" in the fishery in terms of areas and seasons. One of the solutions for reducing bycatch in the fishery is to identify such areas and thereby offer the industry a tool for managing their take of bycatch by minimizing fishing effort in these "hot spots."

Our philosophy has been that consideration of all bycatch as a single entity is not the best approach. Although we felt the need to address the total bycatch in our first analysis, we also wanted to take individual species into consideration. We approached this multispecies aspect of our study using correspondence analysis, which we used to identify the commonly associated species in different zones and areas, as well as the different fates. Our results suggest that this approach can have general appeal not only in identifying areas and species of concern but also in suggesting approaches to solutions. For example, our "hot spot" fishing zone and season were

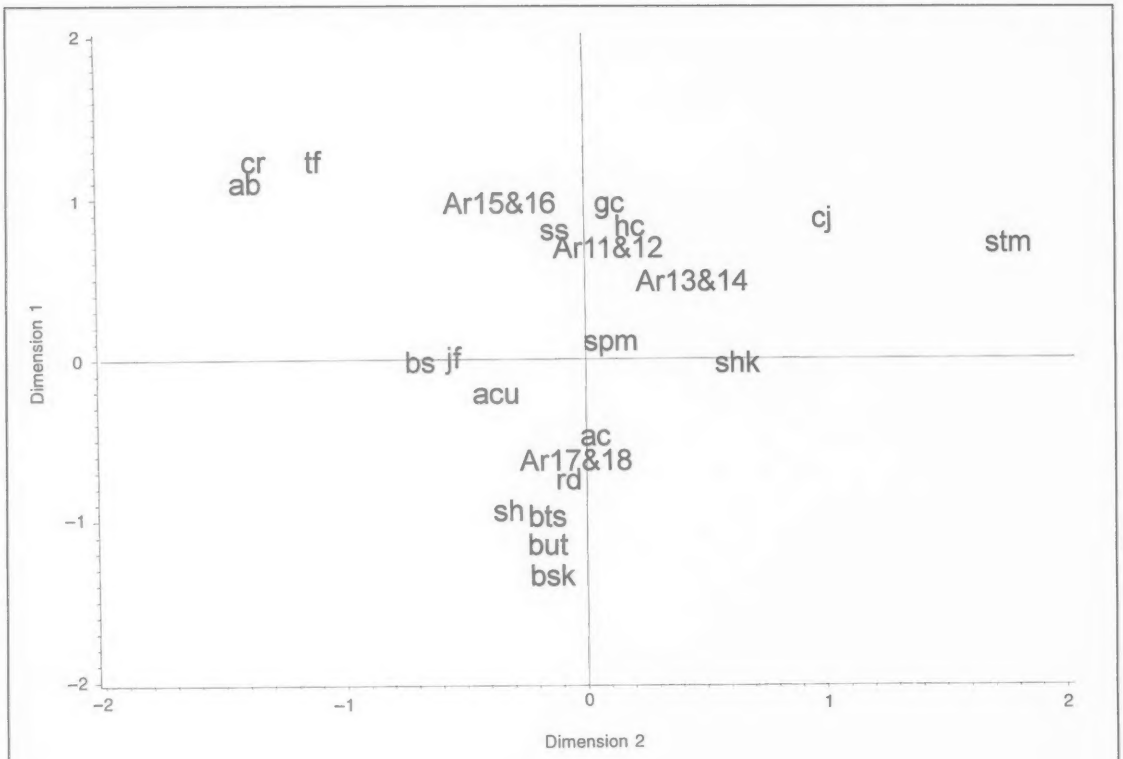

Figure 9

Correspondence analysis plot for species-area associations (fall) for 1995 fishing season.

east of the Mississippi River and April–August. This hot spot was associated with the bycatch of Atlantic croaker, sand seatrout, hardhead catfish, spotted seatrout, and bull sharks. Of these, Atlantic croaker and sand seatrout were the most commonly occurring species in the releasable bycatch and were associated with being gilled. If a reduction in the mortality of these species in the menhaden bycatch were necessary, our study suggests it would require gear modification in the purse seine. A species associated with our hot spot, more likely to require attention, is the bull shark given its life history characteristics. Species-fate associations indicated that bull sharks were primarily associated with being released dead. If a reduction in the mortality of bull sharks as menhaden bycatch were mandated, solutions should be centered around reducing the number of sharks released dead. Rester (1996) has suggested that this could be achieved through modifications to the fish pumping equipment for fish 1 meter in length or larger.

Acknowledgments

We wish to thank the personnel of Gulf of Mexico menhaden industry and members of the Menhaden Advisory Committee, Gulf States Marine Fisheries Commission, for assistance and advice. We wish to thank Donna Rogers, Coastal Fisheries Institute, Louisiana State University, for suggestions and review of the manuscript. We are indebted to James Geaghan, Brian Marx, and Raul Macchiavelli, Department of Experimental Statistics , Louisiana State University, for statistical advice and Steven Branstetter for his review of the manuscript. The manuscript greatly benefitted from the comments of an unknown reviewer and S.X. Cadrin.

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Estimated tuna discard from dolphin, school, and log sets in the eastern tropical Pacific Ocean, 1989–1992

Elizabeth F. Edwards
Peter C. Perkins

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

E-mail address (For Elizabeth Edwards): liz@caliban.ucsd.edu

Abstract.—Pressure to reduce fishery-related dolphin mortality in the tuna purse-seine fishery of the eastern tropical Pacific Ocean (ETP) may alter fishing patterns from the current situation, in which most tuna is caught in association with dolphins, to a situation in which these "dolphin sets" are replaced by sets on unassociated schools of tuna (school sets) or on floating objects (log sets). Although not likely to effect any substantial change in dolphin population dynamics, owing to current low levels of dolphin mortality, such a change in fishing pattern could damage the commercial stock of yellowfin tuna and perhaps stocks of other tuna species because, unlike dolphin sets which generate almost no unwanted catch, school and log sets capture moderate to large amounts of undersized or otherwise undesirable tuna that are subsequently discarded at sea.

In this study, we examined the differences between set types (in short tons of tuna discarded per set by U.S. vessels fishing in the ETP during 1989–92) and then predicted the increase in short tons of tuna discarded per set (all tuna species combined) that would likely result from replacing the dolphin sets with an equivalent number of school or log sets (or both).

Expected discard weight of tuna was 100 times higher for log sets and 10 times higher for school sets than for dolphin sets. Average expected tuna discard per set was 0.06 short tons for dolphin sets, 1.15 short tons for school sets, and 10.5 short tons for log sets. Hypothetically, redistributing all dolphin sets to log sets increased estimated average discard of tuna by the international fleet in the ETP by about 337%.

A hypothetical replacement of all dolphin sets with log sets would lead to estimated discards of 10–25% of the estimated average number of yellowfin recruits to the fishery each year. If this discard is combined with an estimated 25% reduction in tons of yellowfin tuna caught that would result from concommitant changes in size structure of the landed fish (Punsley et al., 1994), the fishery could lose 30–50% of the approximately 98 million individual yellowfin tuna estimated to recruit to the fishery each year. Sustained removals of this magnitude, combined with environmental variability, could pose problems for long-term sustainability of the ETP yellowfin tuna stock; moreover, the change in fishing-effort patterns leading to this effect on yellowfin tuna would likely contribute little to recovery or sustainability of ETP dolphin stocks.

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Fishery Bulletin 96: 210–222 (1998).

Tuna purse-seiners fishing in the eastern tropical Pacific Ocean (ETP) conduct three different types of sets on tuna schools: dolphin sets, school sets, and log sets (IATTC[1,2]). Set types differ only in the technique used to capture the fish; the net used is the same in all cases. Dolphin sets include all sets in which the tuna were captured in association with dolphins. School sets include all sets on tuna schools not associated with either floating objects or with dolphins. "Log" sets as defined in our study include all sets on any floating object encountered by the purse seiner, including natural objects such as trees and tree limbs, dead whales, and other large animals, or other natural debris, as well as human-generated objects such as rafts and discarded trash.

The overwhelming majority of dolphins caught during purse-seining activities in the ETP are caught during dolphin sets, the only set type during which dolphins are captured intentionally. A few dolphins (generally fewer than 25–50) are captured accidentally each year in a few school or log sets or both (generally fewer than 5–10 dolphins), usually because the dolphins were not observed prior to making the set. School sets tend to catch free-swimming schools of moderately small yellowfin tuna, *Thunnus albacares* (about 7–8 kg, 60 cm total length, and not associated with dolphins and with other, unwanted fish), or mixed schools of yellowfin and skipjack tuna (*Katsuwonus pelamis)*, and little else. Dolphin sets catch relatively large yellowfin tuna (15–25 kg and 75–125 cm) associated with dolphins (Punsley[3]), some or (rarely) all of the associated dolphins, and very little else. Log sets have tended historically to catch small, prereproductive yellowfin tuna smaller than about 5 kg and less than about 50 cm fork length or skipjack tuna (or a mixture of both tuna), together with a wide variety and large quantity of other biota including sharks, billfish, other large and small sportfish, and a variety of other small noncommercial tunas.

Dolphin sets traditionally have been preferred by tuna fishermen because the associated yellowfin tuna are abundant, large, relatively easy to locate and capture, not associated with unwanted (nontarget)

[1] IATTC (Inter-American Tropical Tuna Commission) Annual Report. 1988. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 288 p.

[2] IATTC Annual Report. 1990. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 261 p.

[3] More recently (1995 onward), some log sets have begun to capture some bigeye tuna and larger yellowfin although the majority of logs still capture mostly smaller fish. Punsley, R. 1995. Inter-American Tropical Tuna Commission, La Jolla, CA 92038. Personal commun.

fish, and generally have been more valuable per pound than the smaller school- or log-associated tuna. Dolphin sets traditionally have been opposed by conservationists because large numbers of dolphins have died annually as a result of net entanglement during these sets. Fishery-related dolphin mortalities began occurring in the ETP with the advent in the late 1950's and early 1960's of the tuna purse-seine fishery. At that time, new net-hauling equipment and net materials made large-scale purse seining practical for the first time. Within a few years, the earlier practice of catching tuna by pole and line was replaced almost entirely by purse seining. Estimates of dolphin mortality during the 1960's and early 1970's were on the order of 300,000–400,000 dolphins annually. Mortality estimates exceeded 100,000 per year until 1977, when the effects of dolphin mortality limits and improvements in fishing practices finally brought mortality below 50,000 per year. Mortality estimates decreased through 1983 to about 12,000 per year but increased significantly again to over 130,000 in 1986 when U.S. vessels left the ETP to move to the western Pacific and were replaced by vessels from countries with less experience in purse-seining techniques . Following a number of new restrictions on fishing methods and limits on allowable species composition of dolphin mortality, enacted by the U.S. congress in the late 1980's and early 1990's, mortality decreased again to about 25,000 per year in 1991.

Obviously, eliminating dolphin sets would virtually eliminate dolphin captures and associated dolphin mortality in the fishery. Recognizing this simple fact, the U.S. congress in 1992 passed legislation designed to eliminate fishing on dolphins by eliminating the U.S. market for tuna caught in association with dolphins while leaving the market open to tuna caught by other methods in the ETP, i.e. by school and log fishing. It was assumed that all effort previously directed to sets involving dolphins would simply be transferred to sets on schools and logs.

It is probably fortunate for the commercial stock of yellowfin tuna in the ETP, as well as for a host of other species, that the legislation did not affect the fishery in the manner expected. More or less concurrent with the changes in U.S. laws, the majority of the countries practicing purse-seining in the ETP, with the help and leadership of the Inter-American Tropical Tuna Commission, formed in 1992 a voluntary agreement (the Panama Declaration) to limit dolphin mortality dramatically in the tuna fishery. A major factor influencing the remarkable success of this program was the introduction of dolphin mortality limits on a per-vessel basis. Under this system, the total mortality quota for a given year is divided equally among all the vessels fishing that year. In addition, annual quotas were adopted that decreased annually to zero mortality by the year 2005.

Results during the first year that this system was fully operational (1993) far exceeded the stated limits of the Panama Declaration (annual mortality quota of 15,000 dolphins). Annual dolphin mortality during 1993 dropped to about 3,600 animals. Annual dolphin mortality has continued to decrease since then, to less than 2,600 animals during 1996. This decrease in mortality was not accomplished by decreasing the number of sets on dolphins, but rather by significantly decreasing dolphin mortality per set, from about 5 animals per set in 1986 to about 0.3 per set in 1996. The number of dolphin sets remains around 8,000 per year, down only about 20% from the approximately 10,000 sets per year that were practiced from the early 1970's through the early 1990's. At the current time, annual dolphin mortality is between 0.1% and 0.2% of estimated abundances of all dolphin stocks affected by the fishery, compared with annual net reproductive rates of 2–4% per year. Thus, fishery-related dolphin mortality at present is negligible compared with estimated current abundances and replacement rates.

This decrease in dolphin mortality, achieved by decreasing kill-per-set rather than decreasing the number of dolphin sets, has probably been fortunate for the commercial stock of yellowfin tuna and other biota in the ETP because it has apparently forestalled any major shift of fishing effort from dolphin sets to school or log sets.

The remainder of this paper focuses on the potential changes in tuna bycatch (discard) that could have been expected had dolphin set effort actually been transferred to school and log sets. We focus on tuna discard because bycatch data for tuna were the only available data to us when this study began.[4] Provided that the currently low levels of dolphin mortality are maintained, so that maintaining effort on dolphin sets does not appear to endanger dolphin population status or dynamics, the results presented here imply that encouraging such a change in effort patterns would be ecologically unsound.

This study presents the first report characterizing patterns and extent of tuna discard from the U.S. tuna purse-seine fishery in the ETP. We describe here general characteristics of the discard data available to us and apply statistical methods described elsewhere (Perkins and Edwards, 1996) to estimate average discard per set for each set type. We use these estimates of discard per set to estimate average an-

[4] The Inter-American Tropical Tuna Commission initiated in 1993 a large-scale bycatch monitoring program in the ETP, but those data are still being collected and analyzed by that agency.

nual discard by the U.S. fleet during the study period (1989–92) for observed patterns and to predict discards that would have resulted if sets on dolphins were redirected to school or log sets. We then predict annual average discard from the international fleet (of which the U.S. was only a small part) under the same redistributions of effort and discard rates assumed for the U.S. fleet.

Although providing the ultimate impetus for the current study, we consider here only briefly the change in dolphin bycatch that would result from replacing dolphin sets with school and log sets because the effect is quite easy to estimate and is currently almost irrelevant in terms of dolphin population dynamics. The effect is easy to estimate because dolphin mortality is almost nonexistent in school and log sets. Thus replacing dolphin sets with school or log sets (or both) will virtually eliminate fishery-related dolphin deaths. This result is irrelevant in a population dynamics sense because annual fishery-related dolphin mortality is currently less than 5% of estimated annual replacement rates (compared with dolphin mortality rates approaching 100% of annual replacement rates during most years prior to 1993). Current mortality levels are about 2,600 dolphins per year from a variety of stocks composing an overall abundance of about 9.5 million dolphins in the ETP. Even for the stock most commonly affected by the fishery, the northeastern spotted dolphin (*Stenella attenuata*), current kill levels are about 800/year from a stock of about 700,000 animals with an estimated replacement rate of 14,000–28,000 animals/year.

Thus, replacing all dolphin sets with school or log sets would likely have little effect on dolphin stock dynamics, given current levels of fishery-related mortality. However, it appears very likely from our analysis that such a replacement could substantially reduce the abundance and biomass of the commercial tuna stock by substantially increasing the bycatch of yellowfin tuna that are too small for market sale. Discarding these small fish affects both current catch and future size composition. Thus we focus here on the potentially detrimental effects on the commercial stock of ETP yellowfin tuna that could result from redirecting dolphin sets to school and log sets, rather than on the negligible effects such effort changes are likely to have on ETP dolphin stock dynamics.

Methods

Data collection

As part of a bycatch study initiated in 1989 by the Inter-American Tropical Tuna Commission (IATTC), data were collected by scientific observers from either the National Marine Fisheries Service (NMFS) or IATTC, placed aboard U.S. tuna purse seiners during routine fishing trips to the ETP. Observed purse seiners included only those with greater than 400 short-t holding capacity. Those with a smaller capacity do operate in the ETP and are numerous for some countries but are not included in the ETP observer program (IATTC[1,2,5,6]).

Each agency contributed about 50% of the observers. Agencies alternated sending observers on departing trips. Observers recorded time, position, and set type of all sets made by U.S. vessels during the 31-month "study period" from 1 September 1989 through 30 March 1992. Position data were used to allocate each set to one of three geographic areas of fishing effort, as explained below.

Short tons of tuna discarded per set was calculated by subtracting the reported "total tons tuna loaded" from the reported " total tons tuna captured." After completing the original analysis of these data (Perkins and Edwards, 1996), we were informed that the data set we had been provided for analysis did not distinguish between true discard and those cases in which the calculated discard also included some tuna that were transferred to another vessel rather than loaded by the capture vessel because the capture vessel had reached capacity during that set. Thus in our original analysis we missed a small number of sets in which some of the captured fish were transferred to another vessel and became part of the commercial catch rather than discard. We recalculated the discard estimates for this paper using the corrected data; therefore the estimated average discard (and associated parameters) reported here differ slightly from our earlier paper. Because the problem occurred in only a few sets, it led to very little change between the estimated model parameters presented in Perkins and Edwards (1996) and those presented here. The largest change (approximately 10%) occurred in the parameter μ for estimating discard from dolphin sets, but this change has almost no effect on subsequent analyses or conclusions because so little discard overall occurs from dolphin sets.

Observers recorded discard data for only 50% of the sets made during the period 1 September 1989 through 30 July 1990 because only IATTC observers were collecting discard data during this period. During the remaining period, 1 August 1990 through 30

[5] IATTC Annual Rep. 1991. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 271 p.

[6] IATTC Annual Rep. 1992. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 315 p.

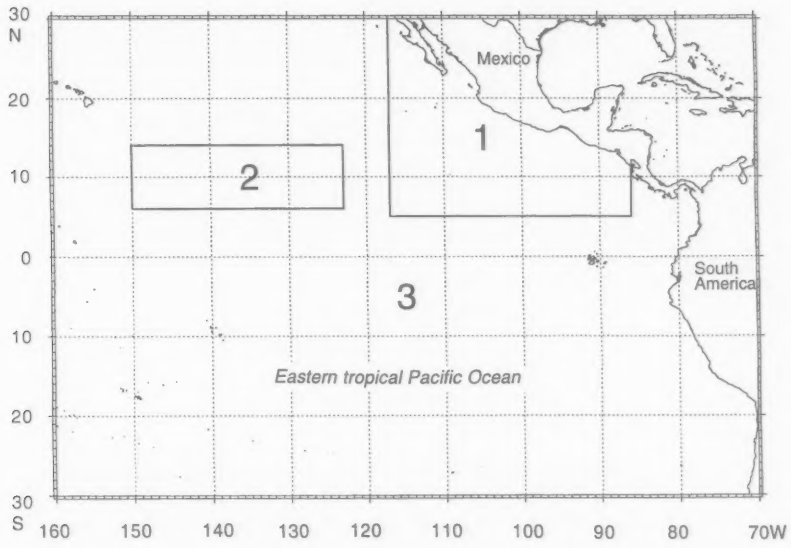

Figure 1

Geographic strata used in estimating average annual discard per set by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92.

March 1992, observers from both agencies collected discard data for all observed sets. Because complete records of discard were missing for the early part of the study period, it was necessary to estimate discard during the study period rather than to measure it directly.

Complete details of data collection and statistical modeling methods and rationale appear in Perkins and Edwards (1996). In summary, we chose to model the data using a modified negative binomial (NB) distribution (the negative binomial with added zeros, Johnson and Kotz, 1969) because this distribution was sufficiently flexible to describe with a single form the disparate catch per set distributions for the three set types. The modified NB was able to accommodate the preponderance of zeros and the long tails (extreme skewness) in the dolphin-set and school-set discard data as well as the more strictly negative binomial distribution of the discard data from log sets.

Readily apparent differences in tuna discard per set type in different areas contributed to our stratification of the data into three geographic areas (Fig. 1), the same areas used currently to determine comparability of U.S. and non-U.S. dolphin mortality rates (Federal Register, 1989). For the purposes of estimating overall discard rates, we ignored school and log fishing in area 2 because no school sets and only ten log sets occurred there (Table 1).

Table 1

Effort data (number of sets on logs, schools, and dolphins) for the U.S. tuna purse-seine fishery in the eastern tropical Pacific Ocean 1989–92. Geographic areas as defined in Federal Register (1989). N = number of sets in a given area, n = number of sets examined for discard, and n^+ = number of sets examined for discard in which discard actually occurred.

Set type	Area		N	n	$n+$
Dolphin	1		2,496	1,445	10
	2		498	272	5
	3		596	393	4
		Total	3,590	2,110	19
School	1		399	279	32
	2		0	0	0
	3		867	681	48
		Total	1,266	960	80
Log	1		537	326	257
	2		10	4	4
	3		791	672	393
		Total	1,338	1,002	654

There was no distinct difference in discard rates among months for any of the three set types, and we did not include a monthly or seasonal effect in our analyses. Although the sample of sets was unbalanced with respect to months (i.e. the period Sep-

tember through March occurred three times during the study period, whereas the period April through August occurred only twice), the magnitude of the imbalance during the study period was not large. Data were too few to examine any annual effects.

We used maximum-likelihood estimates of model parameters from the best-fit models to estimate expected discard per set for each set type. We calculated estimates for individual geographic areas where model fits indicated significant areal effects on parameter values (i.e. for school and log sets), then calculated a "pooled" estimate of expected discard per set from the area-specific estimates. Where no areal stratification was appropriate (i.e. for dolphin sets), we calculated only one "pooled" estimate using the maximum-likelihood estimates of parameter values for the unstratified model.

We estimated standard errors for expected discard per set by bootstrapping rather than by using analytic formulae because only bootstrap methods could be efficiently applied to all three set types. Analytic methods could be easily applied only in the case where no areal stratification was appropriate (i.e. dolphin sets, where we fitted a single model for all areas) and in the case where complete areal stratification was appropriate (i.e. log sets, where we fit separate models in each of the geographic areas).

We estimated annual discard and standard errors of those estimates for the U.S. fleet as observed during the study period by multiplying the estimated overall discard rate for each set type by the corresponding average annual number of sets.

To investigate the effect of entirely eliminating dolphin sets, we predicted potential discard after redirecting all dolphin sets to school or log sets (or both). We used three hypothetical redistributions: 1) all dolphin sets were reassigned to school sets; 2) half of dolphin sets were reassigned to school sets, the remaining half were reassigned to log sets; and 3) all dolphin sets were reassigned to log sets. Sets were reassigned in proportion to the observed proportions of set types by the U.S. fleet in each geographic area; therefore the pooled estimates of expected discard per set could be used for each set type.[7]

We predicted total redistributed discard during the study period by multiplying pooled estimates of expected discard per set for school and log sets by the redistributed number of sets for each type. This procedure assumes that the redirected effort did not change the fishing habits, geographic patterns of the fleet, or the discard per set realized during the redirected effort.

[7] The geographic distribution of set types by U.S. vessels tends to differ from the geographic distribution with international fleet as a whole because U.S. vessels are largely restricted from the nearshore Exclusive Economic Zones (EEZ's) of coastal nations. If data for the geographic distribution of effort by the international fleet had been available, it would have been more appropriate to use that. However, the general results of the present study would likely remain unchanged (see "Caveats" in "Discussion" section).

Results

Patterns in set-type distributions

Several patterns are evident in the number of sets of each type. During the study period, about half the sets by U.S. boats were made on dolphins, about one quarter were made on school sets, and one quarter on log sets (Table 1). Sets were most common in the relatively nearshore area 1, rare in the offshore equatorial area 2, and moderate in the remaining area 3. Only dolphin sets were made with any frequency in area 2 (Table 1; Fig. 2). All three set types were common in areas 1 and 3.

About 70% of school sets were observed in area 3 (Table 1: Fig. 2). Of those sets, most occurred during April and May (59% of sets), between the hours of 8 am and 4 pm local time (68% of sets). Observed school sets in area 1 also occurred primarily between 8 am and 4 pm (76% of sets) but were distributed more homogeneously throughout the year and were much less common than in area 3. No school sets were observed in area 2.

Log sets were also observed primarily in area 3 (58% of sets, Table 1), although fewer sets were observed here during the period June–September (Fig. 2). Observed log sets decreased during summer and winter months in area 1. Log sets usually occurred early in the day in all areas (80% before noon, 56% before 8 am, Fig. 2). Less than 1% of observed log-set effort occurred in area 2.

Contrary to school-set and log-set effort, dolphin sets were observed primarily in area 1 (66% of sets, Table 1) with a small but important number of sets observed in area 2 (17% of sets). Effort in area 2 obviously replaced effort in area 1 during the months of June and July (Fig. 2). Only 1.6% of effort in area 1 but 78% of effort in area 2 occurred during these two months, and all effort in area 2 occurred between June and October. In all three areas, dolphin sets were observed primarily (79%) between the hours of 8 am and 4 pm during which greater effort was evident before noon.

Discard patterns

Estimated tuna discard from U.S. vessels was recorded for 59% (Table 1) of observed dolphin sets,

76% of observed school sets, and 75% of observed log sets. The set data reported 134, 1,098, and 9,819 tons of observed discard, respectively. A nonzero amount of discard was reported in 65% (Table 1) of log sets where discard was recorded, but in only 8% of school sets and only 0.7% of dolphin sets where discard was recorded. Frequency distributions for tons of tuna discarded per set were clustered near zero for dolphin sets, were somewhat wider for school sets, and were much wider for log sets (Fig. 3), indicating the increasing frequency and increasing tonnage of tuna discard from dolphin, school, and log sets, respectively.

Geographic patterns in discard reflected geographic patterns in effort devoted to the three different set types. Both effort and positive discard occurred most frequently in area 1 for dolphin sets and in area 3 for school and log sets (Table 1).

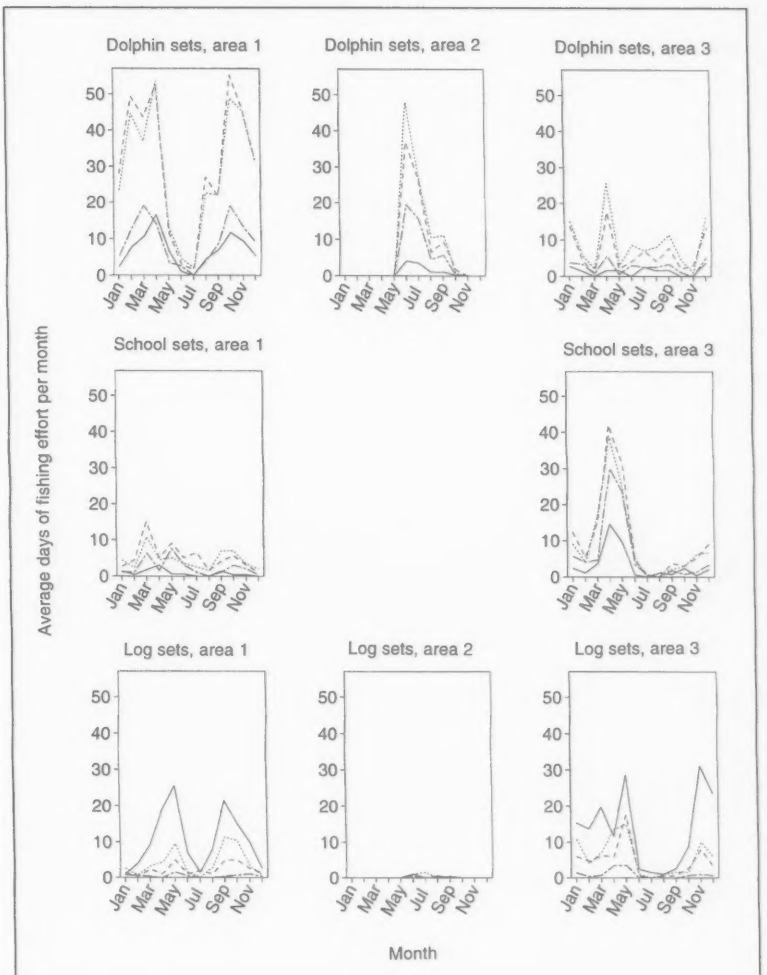

Figure 2

Daily, monthly, and geographic (areas 1, 2, and 3) patterns in fishing effort (number of sets) made on dolphin, school, and log sets by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Solid line = before 0800 hours, dotted line = 0800–1200 hours, dashed line = 1200–1600 hours, and dot-dashed line = after 1600 hours.

Expected discard per set

Expected discard per set for log sets was 10.5 short tons of tuna (all tuna species combined; SE= 0.83, n=998, means range 7.1–15.4 short-t depending on geographic area; Fig. 4). Expected discard per set for school sets was 1.15 short tons of tuna (SE=0.24, n=960, means range 0.97–1.57 short-t) depending on geographic area). Expected discard per set for dolphin sets was 0.06 short tons of tuna (SE=0.2, n=2,110 fishery wide).

Estimated average annual discard

Despite the much larger number of sets (greater fishing effort) on dolphins than on school or logs (Table 1), estimated average annual discard was much greater for log sets than for school or dolphin sets, reflecting the enormous difference between set types in expected discard per set. Estimated average annual discard for the entire U.S. fleet during the study period was 88 short tons per year (SE=29, n=2,110) from dolphin sets, 595 short tons per year (SE=125, n=960) from school sets, and 5,400 short tons of tuna (all species combined) per year (SE=426, n=998) from log sets, based on observed patterns of effort (Fig. 5).

Redistributing the great number of dolphin sets to either of the other set types considerably increased predicted annual discard of tuna from school or log sets (or both), and from the U.S. fleet as a whole.

Redistributing all dolphins sets to school sets increased predicted annual discard of tuna from school

sets by the U.S. fleet from 595 to 2,190 short tons per year. Redistributing all dolphin sets to log sets had by far the greatest effect, increasing predicted annual discard of tuna from log sets by the U.S. fleet from 5,400 to 19,900 short tons.

Predicted total annual discards of tuna from the U.S. fleet for all set types combined were 7,500, 14,000, and 20,500 short tons for redistribution of dolphin sets to all school sets, combined school and log sets, and all log sets, respectively (Fig. 5), representing increases of 1.25 (7,580/6,080), 2.31 (14,000/6,080), and 3.34 (20,500/6,080) times, respectively.

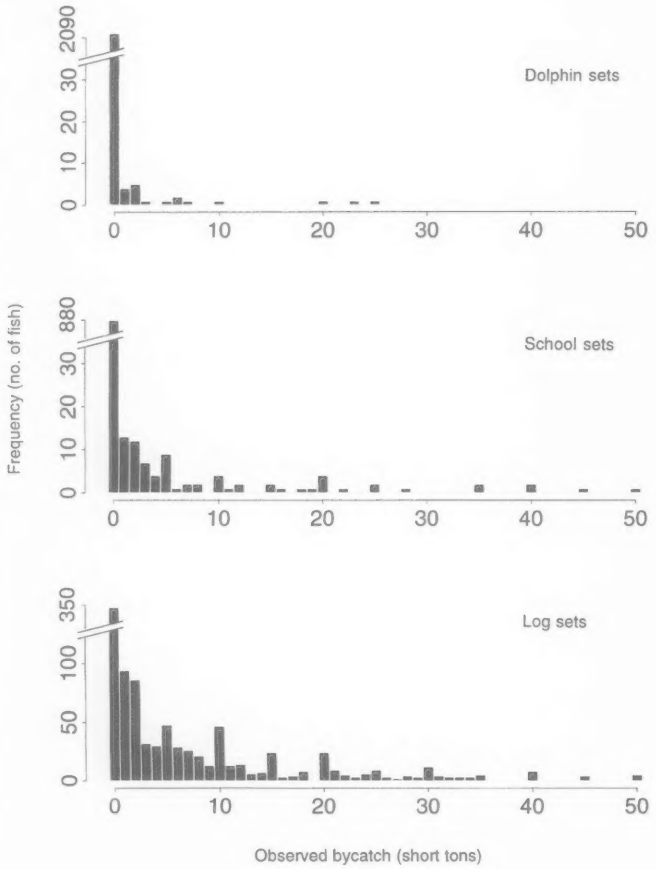

Figure 3

Frequency distributions of observed discard per set for dolphin, school, and log sets by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. The scale for school sets does not show 3 school sets exceeding 50 short tons per set, totaling 310 short tons, and representing 30% of total catch on school sets, with maximum catch per school set = 150 short tons. The scale for log sets does not show 25 sets exceeding 50 tons per set, totaling 3,221 short tons, and representing 33% of the total catch on log sets, with maximum catch per log set = 325 short tons.

Discussion

Comparison with other discard data

Although the data used in this report consist of estimates made "by eye" (i.e. estimated by visually noting the volume of discarded tuna and mentally comparing that volume to the volume of tuna in some container of known size, e.g. the vessel's brailer) and could not be analyzed in hindsight for inter-observer reliability, our results are reasonably similar in magnitude, especially in relative magnitude (expressed as tonnages) between set types, to data collected during 1993 and 1994 by the IATTC as part of a greatly expanded bycatch sampling program in the ETP. Average short tons of tuna discarded per set during these 2 years for dolphin, school, and log sets was 0.17 (no difference between years), 0.58 (0.5 in 1993, 0.9 in 1994), and 8.3 (5 in 1993, 11 in 1994), respectively (Hall[8]). These values are reasonably comparable to our estimates of 0.06, 1.2, and 10.5 short tons of tuna discard per set for dolphin, school, and log sets, respectively. The apparently large differences between the IATTC and NMFS estimates for dolphin sets, and to some extent for school sets, are relatively unimportant because the overall discards for these set types are so low. In addition, annual differences can be substantial although still low in relation to log sets.

Implications for the ETP yellowfin fishery

Our results imply that historically, tuna discard from the U.S. tuna

[8] Hall, M. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038. Personal commun.

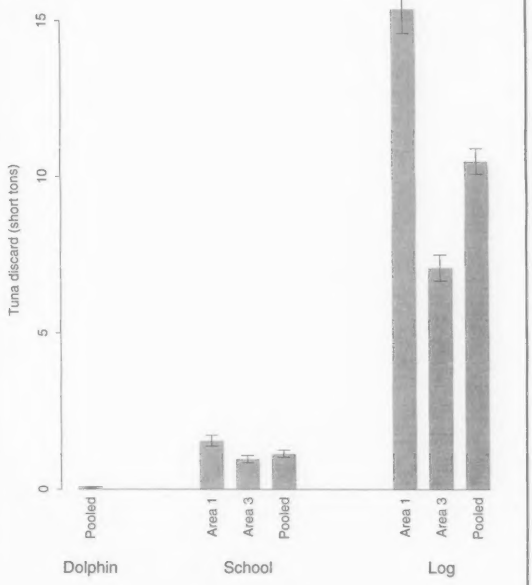

Figure 4

Estimated expected tuna discard per set by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, in specified geographic strata (Federal Register, 1989) and in all areas pooled. Standard errors indicated by vertical bars.

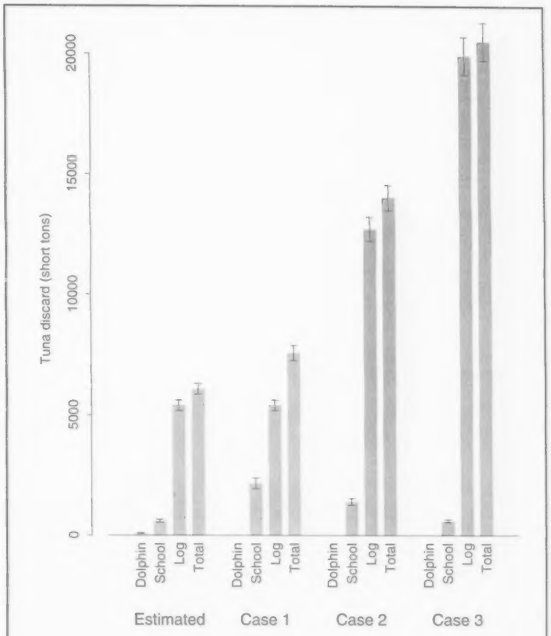

Figure 5

Estimated annual tuna discard by the US tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, under observed effort patterns and redistributed effort patterns where all dolphin sets were redistributed exclusively to school sets (case 1), equally to school and log sets (case 2), and exclusively to log sets (case 3).

purse-seine fleet in the ETP was probably relatively minor (although local effects might have been large at some times). From the fishery's inception in the early 1960's through the mid-1980's, the majority of U.S. vessels (which during that period represented over 90% of the international fleet) targeted tuna associated with dolphins, a strategy that generates very little tuna discard.

The situation has changed dramatically in the past few years, in particular since 1) passage, in 1988, of stringent new amendments to the Marine Mammal Protection Act, 2) the decision by U.S. canneries in April 1990 to buy only "dolphin-safe" tuna, and 3) the passage of the International Dolphin Conservation Act of 1992 (IDCA). The 1988 amendments required non-U.S. fleets to meet strict comparability criteria related to dolphin mortality rates in order to export tuna to the U.S. The cannery decision for dolphin-safe tuna (adopted also by European Community nations in 1993) means that the canneries involved will now buy only tuna that is certified not to have been caught either in association with dolphins or by drift gill nets on the high seas. The IDCA places increasing pressure on both U.S. and non-U.S. fleets to reduce dolphin mortality and to eliminate it altogether by 1999.

Largely in response to these events, most U.S. vessels have left the ETP, either to change flags, retire from fishing altogether, or to fish in the western Pacific Ocean under license from various island nations. Of those U.S. vessels remaining (4 vessels in 1994), all fish on school and floating logs. This change to school and log fishing will have greatly increased the U.S. discard of small immature tuna, although the overall effect on the tuna stocks due to changes in fishing practices by the U.S. fleet is probably small because very few U.S. vessels are currently fishing for tuna in the ETP using any of these set types.

However, the decrease in the size of the U.S. fleet has been offset by increases in the sizes of non-U.S. fleets so that the overall size of the international fleet has remained relatively constant since the mid-1980's. Although many of the non-U.S. vessels are still fishing "on dolphin," increasing numbers of vessels changed during the study period to school and

log fishing in response to pressures from the canneries, the MMPA, and the IDCA. Because all large ETP purse-seiners use the same type of gear, fishing procedures, and vessels, a rough estimate of tuna discard for the entire international fleet can be obtained by simply applying the ratio of discard of total catch for the U.S. fleet to total catches reported for the international fleet, under the assumption that non-U.S. fleets discarded tuna in the same manner as the U.S. fleet[9] during the study period.

Average annual commercial catch (short tons landed, all tuna species combined) by U.S. vessels fishing in the ETP during 1989–91 was 76,425 short tons.[10] Estimated average annual discard for the U.S. fleet during the study period was 6,080 short tons. Thus, estimated total annual discard by the U.S. fleet under observed patterns of effort was 7.96% (6,080/76,425 × 100) of the average annual commercial catch (Hall[11]). As noted previously, predicted total annual discards from the U.S. fleet for redistributions of dolphin sets to log or school sets (or both) increased predicted total discard by 1.25 times for redistribution to school sets, 2.31 times for redistribution to a combination of log and school sets, and 3.37 times for redistribution to log sets (Fig. 5).

Average annual commercial catch for the international fleet during the study period was 395,768 short tons.[12] If observed effort patterns of the U.S. fleet during the period were the same as effort patterns of the international fleet, then discard from the international fleet under hypothetical redistributions of dolphin effort can be simply estimated as 7.96% of 395,768 short tons, i.e. 31,500 short tons. Assuming that changes in effort would affect discard in the same way for the international fleet as for the U.S. fleet, then discard under hypothetical redistributions of dolphin effort can be predicted as 1.25 times, 2.31 times, and 3.37 times 31,500 short tons, for redistributions to all school sets, combined school and log sets, and all log sets, respectively. The predictions are then 39,200, 72,700, and 106,000 short tons of tuna discarded, respectively (Fig. 6).

The significance of these discard predictions for future tuna resources depends on their magnitude in relation to the total stocks of tuna in the ETP. Although the amount of tuna that is potentially discarded appears high, it will not be particularly important if it represents only a few percent of the to-

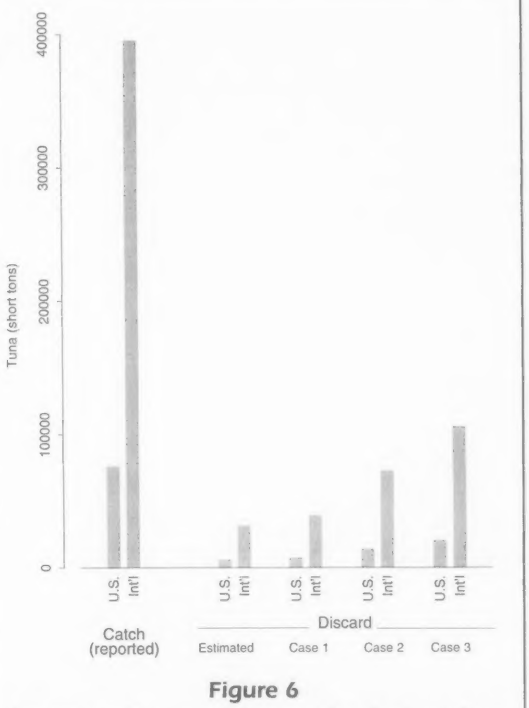

Figure 6

Average annual commercial tuna catch and estimated average annual tuna discard by the U.S. and international purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, under observed effort patterns and redistributed effort patterns where all dolphin sets were redistributed exclusively to school sets (case 1), equally to school and log sets (case 2), and exclusively to log sets (case 3).

[9] Although we cannot test this assumption at present, presumably all vessels selling fish to canneries serving international markets have the same constraints on acceptable sizes for individual tuna retained for sale. It is possible that smaller sizes may be acceptable by canneries located in individual countries, but we are not aware of any such policy. The implications for population dynamics of affected tuna will be the same regardless of whether the fish are marketed or not (they are removed from the population in either case).

We also assume here that the effort distribution is the same for both the international and U.S. fleets. That is not strictly true, but the main difference tends to be that the international fleet, composed mostly of Mexican vessels, fishes more inshore areas (i.e. more in area 1) than does the U.S. fleet alone. Fishing more inshore would increase the fraction of school and log sets in the data. Thus, extrapolation from the U.S. data will, if anything, underestimate the extent of bycatch on school and logs.

[10] Estimated annual catches of tuna (all species combined, surface fishing only) for the U.S. fleet were 110,981, 79,530, and 38,765 short tons for the years 1989, 1990, and 1991, respectively (IATTC, 1991), averaging 76,425 short tons annually for the period.

[11] This compared well with IATTC data showing 7.4% of all sampled tuna captured during 1993 and 1994 were discarded (13,500 short tons of tuna discarded from 181,422 short tons of tuna caught) (Hall, M. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92037. Unpubl. data).

[12] Estimated annual catches of tuna (all species combined, surface fishing only) for the international fleet were 441015, 407445, and 338,385 short tons for the years 1989, 1990, and 1991 respectively (IATTC[5]), averaging 395,768 short tons annually for the period.

tal fish currently in the ecosystem, or a few percent of annual fishery recruitment (i.e. new young fish becoming vulnerable to purse-seine fishing each year), or individuals from a stock with very short life span and high annual ability to restock. Potential significance of discard calculations can be determined by combining estimates of recruitment with information about the species and size composition of fish discarded. These calculations are a rough estimate of the number of fish discarded (i.e. lost from the future commercial population) in relation to fish available for commercial catch. Estimates of discards of young, small fish are especially important in terms of future resources because these young fish have the most biomass to gain per individual, as well as the greatest reproductive potential.

Data recently collected by the IATTC as part of their bycatch investigations indicate that both the fraction and the size composition of yellowfin tuna discards change dramatically with set type (Hall and Deriso[13]). These data can be used to estimate the numbers of yellowfin tuna discarded under various fishing regimes.

IATTC data show that yellowfin tuna composed 92% (by weight) of tuna discard from dolphin sets, 50% of discard from school sets, and 22% of discard from log sets during the years 1993 and 1994 (Table 2).

[13] Hall, M., and R. Deriso. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA, 92038. Personal commun.

Of this yellowfin tuna discard, small yellowfin tuna (defined as less than 2.5 kg, or 5 lb) discarded from log sets were by far the most serious type of loss, particularly in the scenario where all dolphin-set effort was redistributed to log sets. Although small yellowfin tuna composed only 3% and 17% (by weight) of yellowfin tuna discards from dolphin and school sets, they composed about 76% of the discard from log sets (Table 2).

These data can be used to predict yellowfin tuna discard under different fishing regimes, given the percentage of total effort devoted to each of the set types. Assuming, as before, that effort patterns of the international fleet were similar to effort patterns of the U.S. fleet during the study period, we can use the percentages of total observed discard resulting from each set type in the U.S. fleet to estimate tonnages of discard from each set type for the international fleet during the same period.

Of the total annual discard of 6,080 short tons from the U.S. fleet under observed patterns of effort, 88 short tons (1.44%) resulted from dolphin sets, 595 short tons resulted from school sets (9.78%) and 5,400 short tons resulted from log sets (88.8%). Application of these percentages to the estimated total annual discard of 31,500 short tons of tuna from the international fleet produces estimates of 454 (31,500 × 1.44%), 3,079 (31,500 × 9.78%) and 28,000 (31,500 × 88.8%) short tons of tuna discarded annually from dolphin, school, and log sets by the international fleet (Table 2). The percentages of discard composed of

Table 2

Steps in estimating number of individual yellowfin tuna of different sizes discarded from each set type. "% yellowfin" is the sum of all yellowfin bycatch divided by the sum of all tuna bycatch for the years 1993–94 in the IATTC bycatch data base. "% small yellowfin" is the average of percent values for 1993 and 1994; "% medium yellowfin" and "% large yellowfin" were calculated similarly. "Small" yellowfin are less than 2.5 kg. "Medium" yellowfin are 5–15 kg. "Large" yellowfin are greater than 15 kg. Weights are expressed in short tons.

Set type	Total tuna discard (tons)	% yellowfin	Yellowfin discard (tons)	% small yellowfin	% medium yellowfin	% large yellowfin	Small yellowfin (tons)	Medium yellowfin (tons)	Large yellowfin (tons)
dolphin	475	92	437	3	31	66	13	135	288
school	2,976	50	1,488	17	31	53	253	461	789
log	28,177	22	6,199	76	24	1	4,711	1,488	62

Ranges of percent values:
(left = 1993, right =1994)

Set type	% yellowfin	% small yellowfin	% medium yellowfin	% large yellowfin
dolphin	(92–99)	(1–5)	(20–42)	(57–74)
school	(49–50)	(16–17)	(25–36)	(48–57)
log	(19–29)	(73–78)	(20–27)	(0.2)

yellowfin tuna can be applied to these set-specific tuna tonnages to produce estimates of 418, 1,540, and 6,150 short tons of yellowfin tuna discarded annually by the international fleet, under the assumption of observed U.S. effort patterns (Table 2). These estimates compare reasonably well with estimates of total short tons of yellowfin tuna discarded by the international fleet during 1993 and 1994 of 449–917 short tons from dolphin sets, 606–2,108 short tons from school sets, and 3,802–4,150 short tons from log sets (IATTC[14]).

Yellowfin tuna discards under redistributed patterns of effort can be predicted from tonnages predicted under the different effort regimes. The "worst-case" discards will obviously occur when all dolphin sets are redirected to log sets. The total tonnage of tuna discard in this circumstance is the sum of discards from dolphin sets (by definition 0, because we redistributed the dolphin sets effort to log sets), school sets (3,080 short tons, the same as under observed effort patterns because school effort is assumed to be unchanged), and log sets (103,000 short tons; estimated as log discard from observed patterns, 28,000 short tons, multiplied by 3.69, the increase factor for discard observed in U.S. data when redistributing all dolphin sets to log sets). The tonnage of yellowfin tuna in each of these set categories is $0 \times 0.92 = 0$ short tons for dolphin sets, $3080 \times 0.5 = 1{,}540$ short tons for school sets, and $103{,}000 \times 0.22 = 22{,}700$ short tons for log sets, with the "fraction yellowfin" from IATTC's data base.

Obviously, changing entirely from dolphin sets to an equal number of log sets dramatically increases predicted total bycatch of yellowfin tuna. A particularly unfortunate feature of this increase is the number of small yellowfin tuna involved; the vast majority of log-set yellowfin tuna discards are new recruits to the fishery that have grown just large enough to be caught in the seine (Table 2). This increase in yellowfin tuna bycatch is unfortunate for two reasons: first, removing these small fish removes their potential to grow larger and more valuable, thus reducing overall yield per recruit for the fishery (Punsly et al., 1994); second, these small fish are prereproductive. No stock-recruitment relationship has yet been demonstrated for yellowfin tuna in the ETP, but if one exists, these increased losses to bycatch might become troublesome over long periods of time.

The actual effect of these discards of small fish on future yield per recruit depends on the number discarded in comparison with the number recruited. Fortunately, the annual recruitment of yellowfin tuna has been estimated by the IATTC.[5] The number of small fish discarded can be estimated from the weight discarded by assuming that all small discarded yellowfin are new recruits (Table 2). This is reasonable because the "small" size class of discards is defined in the IATTC bycatch data base as fish less than 2.5 kg (Table 2), and Cole (1980) reported that yellowfin tuna recruit to the ETP tuna purse-seine fishery at sizes ranging from 0.7 to 2.0 kg. Thus a short ton of "small" discarded yellowfin tuna, at 907 kg per ton, should include between 454 and 1,296 individual fish.

According to inferred effort patterns, estimated average annual discard of small yellowfin tuna by the international fleet was 4,950 short tons , representing 2.3–6.4 million fish (Table 2). If all dolphin sets are assumed to be replaced by an equal number of log sets, then predicted discard of small yellowfin tuna increased to 17,562 short tons, representing 8.0–22.7 million fish (0 short tons from dolphin sets plus 262 short tons from school sets plus 17,300 short tons from log sets).

By comparison, the estimated annual recruitment of small yellowfin tuna to the ETP fishery for 1983–91 was 98 million fish (IATTC[5]); thus observed effort patterns may have been generating discards representing 2–7% of total recruitment each year. On the other hand, a redistribution of all dolphin-set effort to log sets could increase discards to 8–24% of annual recruitment, depending on the actual sizes of the discarded fish (smaller fish would lead to greater losses per ton of discard, although the increase in catchability with size in this range suggests that much of the discard might be closer to 2 kg than 0.7 kg).

These estimated discards would occur in addition to an expected 25% reduction in yellowfin tuna catch biomass if all dolphin-fishing effort were redistributed to log-fishing effort (Punsly et al., 1994). By implication, a change entirely to log fishing could reduce yellowfin tuna catch in the ETP by as much as 30–50%. A change to a combination of school and log fishing would be less detrimental, but the actual effect would depend on the ratio of school-set effort to log fishing effort. Historical patterns of purse-seine fishing in the ETP, in which 50% or more of effort was directed to dolphin sets, obviously minimized any removal of new recruits from the fishery. Replacement of the entire dolphin-set effort with log-set effort would reverse that characteristic of the fishery, with potentially troublesome effects. Losses to "observed" recruitment as high as 50% may not be likely (Deriso[15]), but it is not difficult to imagine that sus-

[14] IATTC Third Quarter Report. 1995. Table 10. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[15] It is also possible that a shift to log fishing could make some areas, particularly offshore areas, uneconomical to fish so that

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tained losses of even 30% annually might pose long-term problems for the fishery.

Caveats

Our results are based on a number of assumptions, including among others 1) similarity between effort patterns of the U.S. and international fleets in the ETP and 2) constancy in discard per set within each set type, regardless of changes in ecological or economic forces (e.g. oceanographic conditions, fish prices, or both), proportions of effort devoted to each set type, or times and areas fished. In addition, our study does not address possible limitations on the availability of nondolphin sets, e.g. limitations on the number of available schools or logs, possible changes in fleet sizes with the elimination of dolphin sets (e.g. seiners leaving the ETP), or the possibility of greater emphasis on log fishing through increased use of FAD's (fish aggregating devices). Our analysis also assumes that the catch per vessel, the number of vessels in the fleet, and the geographic distribution of set types would remain constant regardless of the amount of effort expended within each set type.

One or more of these assumptions may be invalid (e.g. Punsly et al., 1994), but at present the effects of violating them cannot be assessed quantitatively. For example, relatively greater effort in area 1 would increase tuna discard more than we have estimated in the present study, but increased competition for logs might decrease overall fishing success. Conversely, increased availability of "logs" (where the population of logs has been increased by deployment of FAD's) could mitigate this competition and lead to an increase in fishing success. Conversely yet again, increased availability of logs might "dilute" the available tuna resource per log, leading to decreased fishing success. The actual system response cannot be ascertained at this time.

In addition, the fine-scale size structure of the discards, particularly from log sets, is unknown. The estimated number of individuals potentially lost per short ton varies by a factor of three; at the lower estimate, only about 8% of recruits would be lost to discard; at the higher estimate, closer to 25% would be lost. More estimates await subsampling studies not yet completed. However, even a moderate estimate of 15% loss per year is difficult to dismiss as unimportant, particularly in combination with the significant increase in landed recruits that will result from increased log fishing.

More detailed data on size structure of the bycatch would also make it possible to address the issue of changes in the discard of medium to large yellowfin tuna that might occur in response to changes in effort distribution. Large and medium yellowfin can only become discard in the event that they grow to medium or large size; increases in log fishing will decrease survival of young yellowfin tuna and decrease the probability that these fish will show up later either as direct catch or as discards. Such detailed size-structure data would also make it possible to translate all discard data to a standardized age, making it easier to compare discards between size classes (e.g. a single 2-year-old yellowfin tuna might be found to be equivalent to 100 or more 6-month-old fish if mortality remained the assumed constant average over time). These more detailed studies should be possible in future given the intensive discard sampling program initiated recently by the IATTC (Deriso).[16]

Conclusions

The work presented here provides only a general overview of the apparent situation based on data available to date, but the implications of our simple study are serious and merit further consideration. Our calculations, although only approximate, imply strongly that a change from dolphin to school or (especially) log fishing (or both), although it might alleviate the problem of dolphin mortality, could have significantly detrimental effects on other components of the eastern tropical Pacific Ocean ecosystem, not the least of which is the commercial resource upon which the fishery rests.

Acknowledgments

We thank Al Jackson, for his help and advice about data collection methods and data form interpretation, and the Inter-American Tropical Tuna Commission, for generously making available their summary data on tuna discards from the ETP tuna purse-seine fleet. We also thank Richard Deriso, Martin Hall, and

[15] *continued*
the predicted redistribution of log and school effort to those areas might not occur. Instead, the fishery would likely contract to more nearshore areas, similar to the situation during the 1960's. Yellowfin tuna resident in the offshore zones would escape all exploitation with the resulting appearance of a much smaller stock—on the order of another 25% reduction in recruitment (Deriso, R. 1995. IATTC, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA, 92038. Personal commun.).

[16] Deriso, R. 1996. IATTC, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Road, La Jolla, CA 92038. Personal commun.

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Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*

Jessica H. Farley
Tim L.O. Davis
CSIRO Division of Marine Research
GPO Box 1538, Hobart, Tasmania 7001, Australia
E-mail address (for Jessica Farley): Jessica.Farley@marine.csiro.au

Abstract.—We investigated the spawning dynamics of southern bluefin tuna, *Thunnus maccoyii*, using ovaries obtained from fish caught on the spawning ground in the northeast Indian Ocean and their main feeding grounds in the Southern Ocean, between October 1992 and June 1995. Only sexually mature southern bluefin tuna were taken on the spawning ground and were caught in every month except July, although relative abundance was low from May to August. Peaks in abundance occurred during October and February. Individuals do not spawn over the whole season, and there is a turnover of fish on the spawning ground. The presence of oocytes in all stages of development and the absence of a hiatus in the oocyte size-frequency distributions between unyolked and early yolked oocytes indicate that southern bluefin tuna have asynchronous oocyte development and indeterminate annual fecundity. The presence of either migratory nucleus or hydrated oocytes and postovulatory follicles in the ovaries of many females indicates that southern bluefin tuna are capable of multiple spawning. On the basis of the proportion of females with postovulatory follicles, it appears that females spawn on average every 1.1 days. The average spawning batch fecundity, estimated from counts of hydrated oocytes, was 6.0 million oocytes or 57 oocytes per gram of body weight.

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Southern bluefin tuna, *Thunnus maccoyii*, are large, migratory pelagic fish with a circumglobal distribution between 30°S and 50°S. Stocks are considered to be overexploited, and parental stocks, in particular, are considered depleted (Caton et al., 1990; Anonymous[1]). Of all the tunas, bluefin tunas (*T. maccoyii* and *T. thunnus*) are the best adapted to cold water (Carey, 1973) and thus are able to occupy the rich feeding grounds of the temperate oceans. However, like other tunas, the early life history of southern bluefin tuna is restricted to warm waters, and the only known spawning area is in the tropical east Indian Ocean where surface water temperatures exceed 24°C during the spawning period (Yukinawa and Miyabe, 1984; Yukinawa, 1987) (Fig. 1). Juveniles leave the spawning grounds within a few months of hatching and move south along the continental shelf of Western Australia. This movement is probably assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981). Juveniles first appear in the warm waters of the Great Australian Bight as one-years-olds in summer and then disperse along the West Wind Drift in winter.

Ichthyoplankton surveys have been used to define southern bluefin tuna spawning grounds and season of spawning. Southern bluefin tuna larvae have been caught within latitudes 7° and 20°S and longitudes 102° and 124°E from September to March (Ueyanagi, 1969; Yonemori and Morita, 1978; Yukinawa and Miyabe, 1984; Nishikawa et al., 1985; Yukinawa and Koido, 1985; Yukinawa, 1987; Davis et al., 1990). However, the northerly limit of spawning is not clear because there has been little sampling effort in Indonesian territorial waters. Apart from a general understanding of the location and timing of spawning and the associated migration patterns, little detailed information is available on the reproductive dynamics of southern bluefin tuna. To understand spawning seasonality, spawning frequency, and batch fecundity with greater accuracy, we analyzed ovarian samples from fish captured on spawning grounds in the northeast Indian Ocean and feeding grounds in the Southern Ocean (in waters off Tasmania, New Zealand, and South Africa)

Materials and methods

Southern bluefin tuna ovaries were obtained from two sources: Indonesian-based longlining vessels fishing on the northern part of the spawning

[1] Anonymous. 1994a. Report of the thirteenth meeting of Australian, Japanese and New Zealand scientists on southern bluefin tuna. Report to management, 20–29 April 1994, Ministry of Agriculture and Fisheries, Wellington, New Zealand, 13 p.

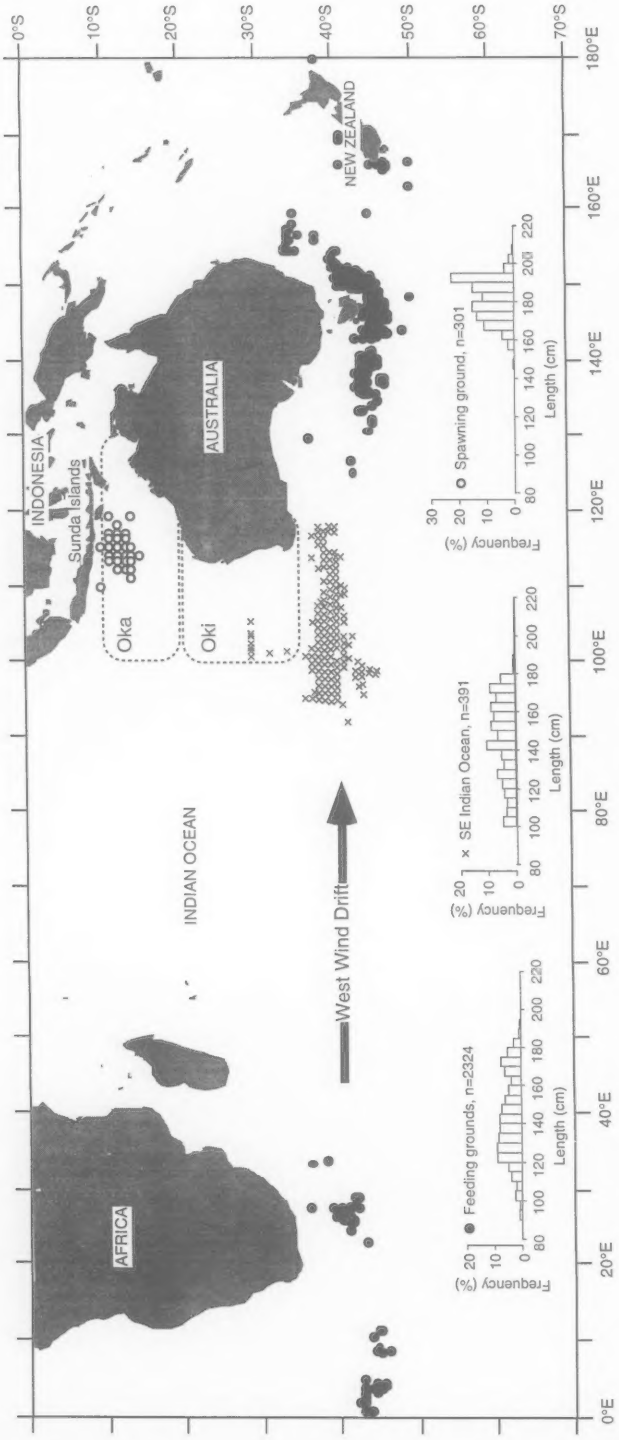

Figure 1

Locations where southern bluefin tuna ovaries were collected. Length-frequency distributions are shown for tuna sampled on the spawning grounds (○) in the northeast Indian Ocean; in the SE Indian Ocean (×) through which the spawning grounds are accessed; and on the feeding grounds along the West Wind Drift (●) in waters off Tasmania, New Zealand, and South Africa. The "Oka" and "Oki" fishing grounds referred to by previous researchers (Kikawa, 1964a, 1964 b; Shingu, 1970) are shown.

ground in the northeast Indian Ocean; and Japanese longine vessels operating in the Southern Ocean (on feeding grounds off Tasmania, New Zealand, and South Africa and on staging grounds in the southeast Indian Ocean) (Fig 1).

The ovaries of 475 females were collected from the complete size range of southern bluefin tuna caught on the spawning ground. Ovaries were removed at sea, labelled, stored on ice, and matched with the corresponding tuna carcass at Benoa in the Sunda Islands. Dressed weight (where fish was gilled, gutted, its fins removed, and its tail stock left intact) was measured to the nearest kg, and fork lengths of most fish to the nearest cm. A subsample was removed from 200 ovaries and fixed in 10% buffered formalin. The ovaries were frozen and flown by airfreight, along with the subsample, to Australia. In addition, up to 30% of all longline catches landed at Benoa were monitored and the individual weights and lengths of southern bluefin tuna were recorded.

Ovaries from the Southern Ocean were collected at sea from the fishing grounds around Tasmania, New Zealand, South Africa, and the southeast Indian Ocean. The areas around Tasmania, New Zealand, and South Africa are considered to be feeding grounds for immature and adult southern bluefin tuna, whereas the southeast Indian Ocean is the area where pre- and postspawning fish are caught during the spawning season. In total, ovaries were collected from 2,340 females from the feeding grounds in the Southern Ocean and from 393 females from the southeast Indian Ocean. Ovaries were frozen immediately after collection. Fork lengths were measured to the nearest cm.

In the laboratory, a core subsample was taken from each ovary while frozen. Subsamples were fixed in 10% buffered formalin, embedded in paraffin, and standard sections were prepared for histological examination (cut to 6 μm and stained with Harris's haematoxylin and eosin). All ovaries collected on the spawning grounds and 53 of the ovaries collected from the Southern Ocean were processed in this way.

Ovaries were thawed, trimmed of fat, blotted dry, and weighed to the nearest g. The mean diameter (random axis to the nearest μm) of five oocytes from the most advanced group of oocytes (MAGO) was determined for each ovary with a video coordinate digitizer connected to an Ikegami video camera mounted on a stereomicroscope at 50× magnification. Gonad index was calculated as

$$GI = W/L^3 \times 10^4,$$

where W = gonad weight in g; and
L = length to caudal fork in cm (Kikawa, 1964a; Shingu, 1970).

All ovaries were examined for residual hydrated oocytes as evidence of spawning activity.

Histological classification and spawning frequency

Because many of the ovaries were frozen before a subsample could be removed, it was necessary to assess whether histological sections prepared from frozen ovarian material could be used to determine gonad stage and spawning activity. A comparison was made between histological sections prepared from 200 ovaries which were subsampled both before and after freezing. Although considerable cell destruction was observed in the histological sections from frozen tissue, oocytes, atretic oocytes, and postovulatory follicles were still distinguishable and could be classified.

Histological sections were classified with criteria similar to those developed for northern anchovy, *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980, 1985a, 1985b), skipjack tuna, *Katsuwonus pelamis* (Hunter et al., 1986) and yellowfin tuna, *Thunnus albacares* (Schaefer, 1996). Each ovary was staged by the most advanced group of oocytes present into one of five classes: unyolked, early yolked, advanced yolked (Fig. 2A), migratory nucleus (Fig. 2B), or hydrated (Fig. 2C). In order to determine the relation between atresia (resorption of oocytes) and spawning, ovaries were also classified by the level of α and β stage of atresia in advanced yolked oocytes. During the α stage of atresia, yolk resorption takes place (Fig. 2D). During the β stage of atresia, the remaining granulosa and thecal cells are reorganized and resorbed leaving a compact structure containing several intercellular vacuoles.

Ovaries were classified into one of the following five atretic states:

0 no α atresia present, but advanced yolked oocytes are;
1 <10% of advanced yolked oocytes are in the α stage of atresia;
2 10–50% of advanced yolked oocytes are in the α stage of atresia;
3 >50% of advanced yolked oocytes are in the α stage of atresia;
4 100% of advanced yolked oocytes are in the α stage of atresia, or no advanced yolked oocytes are present but oocytes in the β stage of atresia are present.

Spawning frequency was determined by the postovulatory follicle method of Hunter and Macewicz (1985a). This method uses the incidence of females with postovulatory follicles less than 24 hours old to define the fraction of the population spawning. Because the time of capture was not available, we could not assign ages to postovulatory follicles based on the estimated time of death relative to the estimated time of spawning. Postovulatory follicles were, therefore, aged according to their state of degeneration with criteria developed for skipjack tuna, yellowfin tuna, and bigeye tuna, *Thunnus obesus* (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996), all of which spawn in water temperatures above 24°C and resorb their postovulatory follicles within 24 hours of spawning. We assumed that southern bluefin tuna resorb postovulatory follicles at the same rate as other tropical spawning tuna because water temperature appears to be the dominant factor governing resorption rates (Fitzhugh and Hettler, 1995). We recorded postovulatory follicles in histological sections according to methods of Hunter and Macewicz (1985a), Hunter et al. (1986) and Schaefer (1996). Postovulatory follicles were classified as either 0 (absent), 1 (new) (Fig. 2E), 2 (less than 12 hours old), 3 (12 to 24 hours old), or 4 (indistinguishable owing to tissue decay). The incidence of females with postovulatory follicles of any age was used to determine spawning frequency.

Females were classified into one of four spawning states depending on the oocytes, atretic state, and postovulatory follicle class present.

1 Immature: Ovaries contain no advanced yolked oocytes or advanced yolked oocytes in the α stage of atresia. No residual hydrated oocytes present.

2 Spawning: Ovary contains advanced yolked oocytes and evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oocytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.

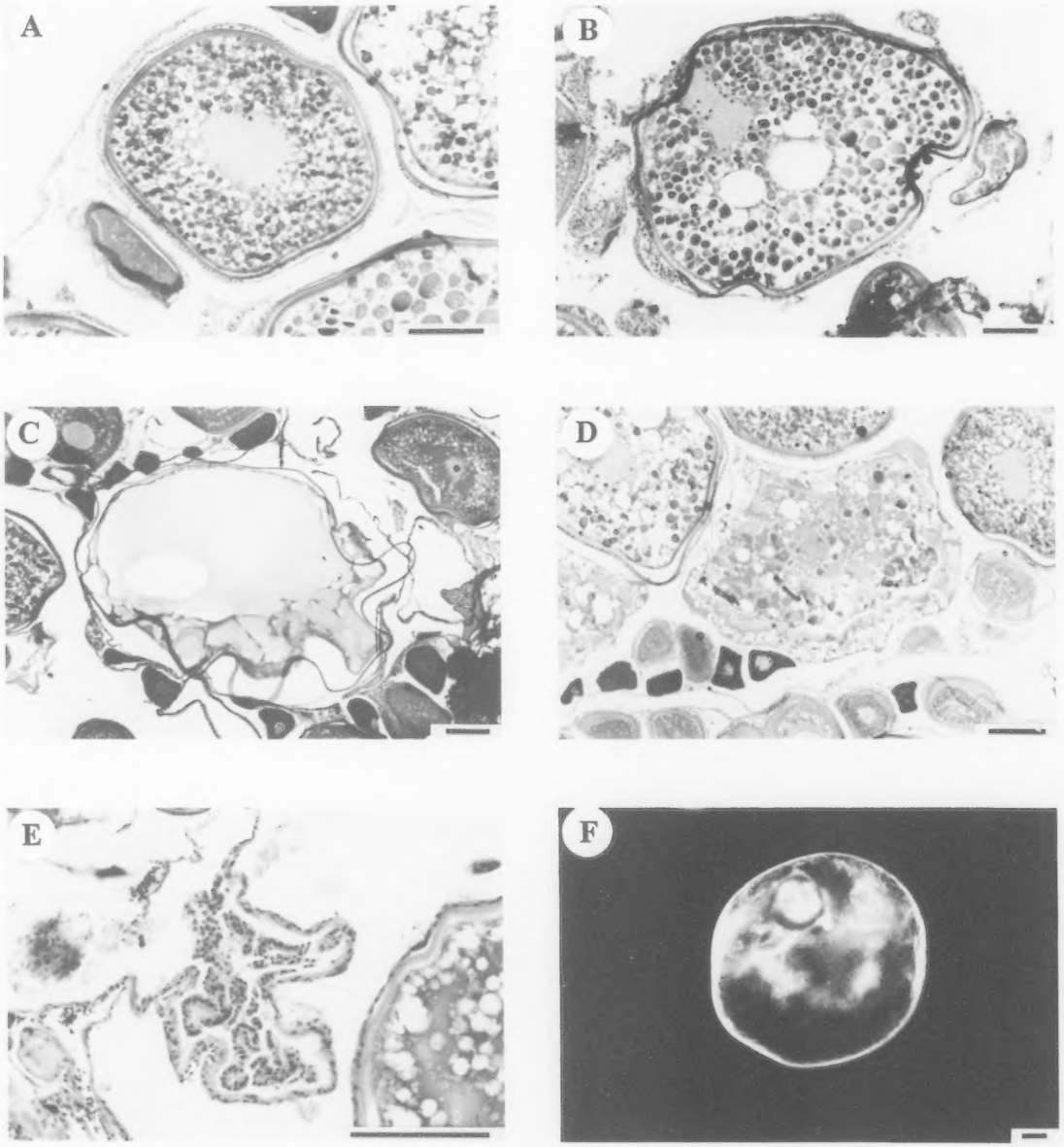

Figure 2

Photomicrographs of southern bluefin tuna, *Thunnus maccoyii*, ovarian tissue collected from the spawning ground (northeast Indian Ocean) between October 1992 and June 1995. (**A–E**) Transverse sections stained with Harris's haematoxylin and eosin. (A) advanced yolked-stage oocyte; (B) migratory-nucleus-stage oocyte; (C) oocyte in the early stages of hydration with some yolk plates still visible; (D) fully yolked oocyte in a stage of α atresia; (E) new postovulatory follicle; (**F**) hydrated-stage whole oocyte. Bar = 0.1 mm.

3 Nonspawning (mature): Ovary contains advanced yolked oocytes but no evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oocytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.
4 Postspawning: Ovaries contain either: 1) >50% of both early and advanced yolked oocytes in the α stage of atresia; 2) 100% of advanced yolked oocytes in the α stage of atresia; or 3) no yolked oocytes are present but oocytes in the β stage of atresia are, and residual hydrated oocytes may or may not be present.

Fecundity

To find out if the annual fecundity of southern bluefin tuna could be determined before spawning began, we measured the distribution of oocyte sizes within ovaries of four females at various stages of maturity. Ovarian subsamples containing at least 1,000 oocytes were removed from each ovary, teased apart, and each oocyte (greater than 100 μm in diameter) was measured in a random orientation to the nearest μm under a stereomicroscope.

We estimated batch fecundity (the number of hydrated oocytes released per spawning) by the gravimetric method (Hunter et al., 1985) for 21 females with unovulated hydrated oocytes (Fig. 2F). A split-plot analysis of variance (ANOVA) was used to determine the appropriate locations to subsample the ovary. The data were structured with 6 fish examined as blocks, ovarian lobe (left or right) as main plots and twelve subsamples as subplot effects. Six subsamples were taken from each ovarian lobe in the anterior, middle, and posterior regions of both lateral sides (Table 1). A significant difference between ovarian lobes was found in the number of hydrated oocytes per gram of total ovary weight and in the lobe × lateral side interaction. Consequently, a subsample of less than 1 g was taken from both sides of each ovarian lobe. Each subsample, consisting of a core from the periphery to the lumen, was weighed to the nearest 0.01 mg and fixed in 10% buffered formalin. Each subsample was teased apart and washed through two sieves, similar to those of Lowerre-Barbieri and Barbieri (1993) to separate out the hydrated oocytes, which were counted under a stereomicroscope. The number of hydrated oocytes per gram of ovary was raised to the weight of both ovaries to give an estimate of batch fecundity for each of the four subsamples.

Results

Ovary maturation

Ovaries obtained from fish on the spawning ground (northeast Indian Ocean), the staging ground (southeast Indian Ocean), and the feeding grounds (Southern Ocean) show clear differences in development based on ovary weight (Fig. 3). Females less than 140 cm showed no or minor ovary development; therefore it appears that they would not spawn in the coming season. The majority of ovaries collected from the feeding grounds weighed less than 1 kg and had a gonad index (GI) of <3.2, whereas ovaries from the southeast Indian Ocean weighed up to 2.8 kg and had GI values up to 4.9. Some of the ovaries of females caught between August and December on the feeding grounds showed signs of maturity, because their MAGO's were in advanced yolked stage with diameters greater than 400 μm. Females from the spawning ground had larger ovaries, weighing up to 7.4 kg. All ovaries from fish collected on the spawning ground had a MAGO diameter greater than 400 μm, except three ovaries with MAGO's between

Table 1

Split-plot ANOVA of the effect of location of tissue sample from southern bluefin tuna, *Thunnus maccoyii*, ovaries on the number of hydrated oocytes per gram of ovary.

Source	df	Sum of squares	Mean square	*F*-value	*P*-value
Blocks					
Fish	5	17,201,897	3,440,380	279.721	<0.001
Main plots					
Lobe	1	168,326	168,326	13.686	0.014
Main plot error	5	61,497	12,299	0.764	0.580
Subplot effect					
Lateral side	1	711	711	0.044	0.834
Region	2	34209	17,104	1.062	0.353
Lateral side × region	2	82,599	41,300	2.565	0.087
Lobe × lateral side	1	152,159	152,159	9.450	0.003
Lobe × region	2	12,944	6,472	0.402	0.671
Lobe × region × lateral side	2	58,207	29,103	1.808	0.175
Subplot error	50	805,044	16,101		

153 and 207 μm. These three female had recently finished spawning because their ovaries contained either 100% of advanced yolked oocytes in an α atretic state or residual hydrated oocytes but no healthy advanced yolked oocytes.

Spawning Season

Southern bluefin tuna were caught on the spawning ground during every month, except July. Catch per unit of effort (CPUE), expressed as the number of fish caught per vessel fishing day, showed that abundance was low from May to August (Fig. 4). In the 1993–94 season, abundance peaked in February, and in the following season, abundance peaked in October and February.

Females with high GI values were caught on the spawning ground during all months that ovaries were collected. Gonad index values were variable, however, ranging from 1.3 to 13.1. There were no peaks or trends during this time. These observations suggest that spawning activity is constant throughout the season.

Histological classification

All ovaries examined histologically from the Southern Ocean were classified as immature, nonspawning (mature), or postspawning. Females greater than 140 cm, with advanced yolked oocytes, collected between August and December were probably prespawners preparing to migrate to the spawning ground. Surprisingly, 78% of these prespawning females had α atresia of advanced yolked oocytes. The level of atresia present was related to ovary weight or GI (Fig. 5). The ovaries of all females with GI's<2 had no or <10% α atresia (atretic states 0 or 1), whereas 80% of females with GI's>2 had 10 to 50% α atresia (atretic state 2). This finding suggests that females begin resorbing yolked oocytes as their ovaries mature. Atresia of unyolked or early yolked oocytes was not observed in these females. Postspawning females were found in the Southern Ocean in all months that ovaries were collected, including both the early and late months of the spawning season (September to December). Ovaries, however, were not collected between January and March from the Southern Ocean.

The ovaries of all females sampled on the spawning ground were classified as mature because they contained either advanced yolked oocytes or oocytes in either an α or β stage of atresia. Of the females, 69.2% were classed as spawning, 30.2% as nonspawning, and the remaining 0.6% as postspawning on the basis of oocyte stage, atretic stage, and postovulatory follicle class present. The mean GI

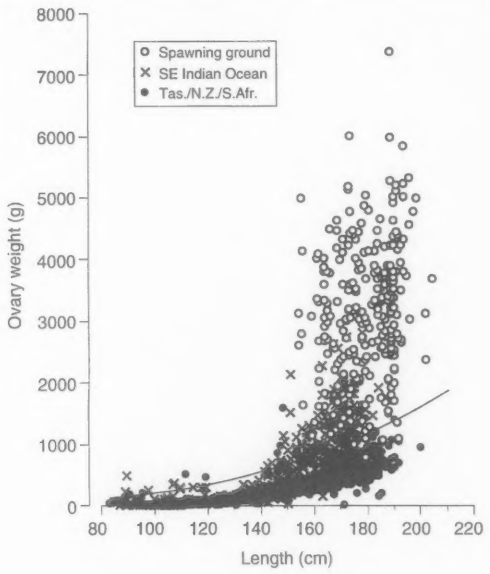

Figure 3

The relation between ovary weight and body length for southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground in the northeast Indian Ocean, on the staging grounds in the southeast Indian Ocean, and on feeding grounds off Tasmania, New Zealand, and South Africa. The line represents a gonad index of 2.

(±95% CI) of spawning and nonspawning females was similar at 5.4 (0.37) and 5.6 (0.29) but GI was not calculated for postspawning females because the sample size was too small (n=3). Spawning and nonspawning females were found on the spawning ground throughout the spawning season. All postspawning females were collected in October. The majority of females identified as spawning (86.1%) had ovaries containing no or less than 10% α atresia. The remaining 13.9% of females identified as spawning contained more than 10% α atresia. Nearly 90% of nonspawning females, however, contained 10–50% of advanced yolked oocytes in an α atretic state. We have used this criterion of <10% α atresia to group fish we considered to be at the height of spawning, which we refer to as "prime spawning condition."

There did not appear to be any seasonal trends in the proportions of each atretic state throughout the spawning season (Fig. 6), suggesting that spawning in southern bluefin tuna is not synchronized. This is confirmed by an absence of an increase in the incidence of postspawning females at the end of the spawning season.

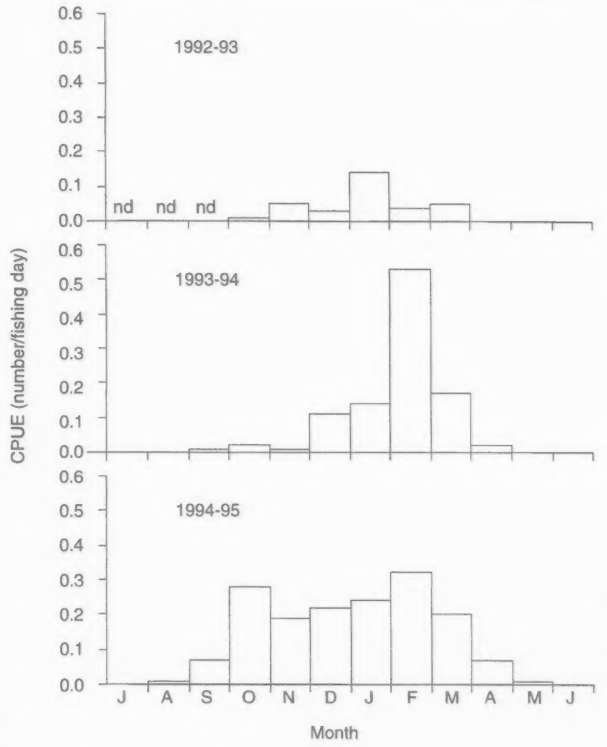

Figure 4

CPUE of southern bluefin tuna, *Thunnus maccoyii*, (number caught per vessel per fishing day) by month for three consecutive spawning seasons. From December 1993, additional companies with higher catch rates were monitored causing an increase in CPUE from that date.

Spawning frequency

The ovaries of 68.7% of females had evidence of recent or imminent spawning activity. The absence of a peak in the percentage of females spawning during the season (Fig. 7) suggests that spawning intensity was constant. The ovaries of 120 females gave evidence of two spawning events, that is, they contained maturing oocytes (either migratory nucleus or hydrated) and postovulatory follicles. The majority of ovaries contained progressively more developed oocytes with progressively older postovulatory follicles. If postovulatory follicles are resorbed within 24 hours of spawning, then southern bluefin tuna are capable of spawning daily.

The fraction of females that spawned per day, measured by the fraction of females with postovulatory follicles, was 0.62 (Table 2). This gave a weighted mean spawning interval of about 1.6 days. If we examine only those females in "prime spawning condition" (<10% α atresia), then the spawning fraction was 0.90 giving a weighted mean interval of 1.1 days. This value suggests that once females start spawning, they spawn daily.

Batch fecundity

The ovaries of nonspawning females collected from the southeast Indian Ocean contained a large number of unyolked oocytes less than 150 μm in diameter (Fig. 8). This number was reduced as females matured during the season and began spawning. Oocytes of all stages were present in the ovary of spawning females; therefore it appears that southern bluefin tuna have an asynchronous pattern of oocyte development. Unlike species with determinate annual fecundity, a gap in the oocyte size-frequency distribution did not appear between unyolked (<200 μm diameter) and early yolked (200 to 400 μm diameter) oocytes (Fig. 8). This finding indicates that advanced yolked oocytes are continually maturing during the spawning season, from the pool of unyolked oocytes, and are spawned. The ovaries of 86% of females identified as spawning contained no or <10% α atresia, indicating that the majority of advanced yolked oocytes that are matured are spawned. Residual hydrated oocytes were found in the ovaries of only 5.6% of females collected from the spawning ground, which suggests that all hydrated oocytes are released at each spawning.

The mean relative batch fecundity and 95% CI's estimated for 20 females of known weight was 56.5 (±16.1) oocytes per gram of body weight. The relation between length (cm) and batch fecundity (BF) was best described by the equation

$$BF = (4.78242 \times 10^{-17}) \times L^{7.530}$$

(F=23.9, df=1,18, P<0.001) (Fig. 9).

However, the relation was highly variable with only 57% of the variance explained by the regression.

Discussion

Spawning ground and season

All female southern bluefin tuna sampled on the spawning ground were mature, and the smallest was

147 cm long. Davis[2] showed that the mean length at which 50% of southern bluefin tuna were mature was around 152 cm based on oocyte diameters>400 μm, and 162 cm based on GI's>2. Warashina and Hisada (1970) considered that southern bluefin tuna caught on the "Oka" grounds (Fig. 1) in the 1960's reached maturity at 130 cm, although reanalysis of these data showed that this was the smallest size at which they matured and that 50% maturity was not reached until 146 cm (Anonymous[3]). Size at maturity appears to have increased progressively since then, being 154 cm in the period 1985–89. The increase in length at maturity can be attributed, in part, to an increase in the growth rate of southern bluefin tuna between the 1960's and 1980's reported by Hearn,[4] because maturity appears to be determined by age rather than length.

[2] Davis, T. L. O. 1995. Size at first maturity of southern bluefin tuna. Council for the conservation of southern bluefin tuna scientific meeting; 10–19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/9, 9 p.

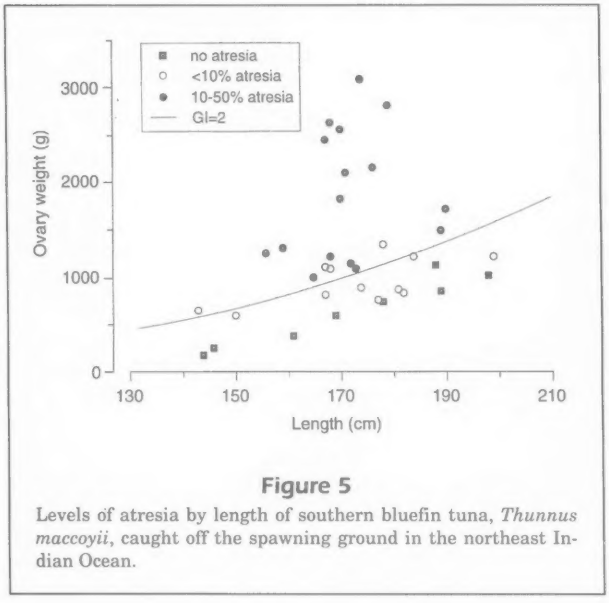

Figure 5

Levels of atresia by length of southern bluefin tuna, *Thunnus maccoyii*, caught off the spawning ground in the northeast Indian Ocean.

The abundance of southern bluefin tuna on the spawning ground was not constant throughout the spawning season. Catch-per-unit-of-effort data indicated that a peak in catches occurred in October for the 1993–94 season and in October and February for the 1994–95 season. Japanese CPUE data also indicate there were two peaks in abundance on the spawning ground in the early years of the fishery; the first in September and October and the second in February and March (Davis and Farley[5]). The reason for two peaks is unknown but could be linked to the widespread distribution of southern bluefin tuna along the feeding grounds of the West Wind Drift. It is possible that the cues for migration to the spawning grounds take place at different times depending on where the fish are prior to spawning. Fish may reach spawning condition earlier in some areas than in others. Also the time needed to migrate to the spawning grounds would differ between areas.

Spawning duration

This study extends the known duration of the spawning season of southern bluefin tuna. Females were caught on the spawning ground in

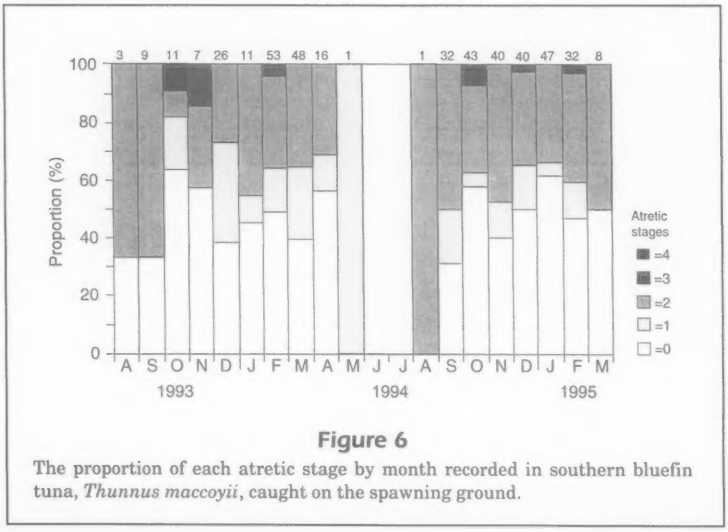

Figure 6

The proportion of each atretic stage by month recorded in southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground.

[3] Anonymous. 1994b. Report of the southern bluefin tuna trilateral workshop, 17 January–4 February 1994, CSIRO, Hobart, Australia, 172 p.

[4] Hearn, W. S. 1994. Models for estimating SBT age at length during the transition period. 13th SBT trilateral scientific meeting; 19–29 April 1994, Wellington, New Zealand. Ministry of Agriculture and Fisheries, Wellington, New Zealand, Rep. SBFWS/94913, 16 p.

[5] Davis, T. L. O., and J. H. Farley. 1995. Catch monitoring of fresh tuna caught by the Bali-based Indonesian/Taiwanese longline fishery. Council for the conservation of southern bluefin tuna scientific meeting; 10–19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/2, 18 p.

Table 2

Spawning fraction and spawning interval of southern bluefin tuna, *Thunnus maccoyii*, by month for all females and females in prime spawning condition collected from the spawning ground between October 1992 and March 1995. POF = postovulatory follicles. *n* = no. of fish in sample.

		All females				Females in prime spawning condition (<10% atresia)			
		n	*n* with POF's	Spawning fraction	Spawning interval (days)	*n*	*n* with POF's	Spawning fraction	Spawning interval (days)
1992	Oct	3	1	0.3	3.0	1	1	1.0	1.0
	Nov	1	1	1.0	1.0	1	1	1.0	1.0
	Dec	1	1	1.0	1.0	1	1	1.0	1.0
1993	Jan	9	8	0.9	1.1	7	7	1.0	1.0
	Feb	3	1	0.3	3.0	2	1	0.5	2.0
	Mar	4	4	1.0	1.0	4	4	1.0	1.0
	Apr	2	0	0.0					
	Aug	3	3	1.0	1.0	1	1	1.0	1.0
	Sep	9	4	0.4	2.3	3	3	1.0	1.0
	Oct	11	8	0.7	1.4	9	8	0.9	1.1
	Nov	7	4	0.6	1.8	4	4	1.0	1.0
	Dec	26	20	0.9	1.1	19	19	1.0	1.0
1994	Jan	11	6	0.5	1.8	6	6	1.0	1.0
	Feb	53	36	0.7	1.5	34	31	0.9	1.1
	Mar	48	31	0.6	1.5	31	28	0.9	1.1
	Apr	16	13	0.8	1.2	11	11	1.0	1.0
	May	1	0	1	0				
	Aug	1	1	1.0	1.0				
	Sep	32	12	0.4	2.7	16	11	0.7	1.5
	Oct	43	26	0.6	1.7	26	22	0.8	1.2
	Nov	40	22	0.6	1.8	21	19	0.9	1.1
	Dec	40	23	0.6	1.7	26	22	0.8	1.2
1995	Jan	47	30	0.6	1.6	31	28	0.9	1.1
	Feb	32	20	0.6	1.6	19	19	1.0	1.0
	Mar	8	3	0.4	2.7	4	3	0.8	1.3
Unknown		16	11	0.7	1.5	8	8	1.0	1.0
Total		467	289	0.62	1.62	287	259	0.90	1.11

all months except July, although the main spawning season appeared to be from September to April when CPUE was highest. Previously, the spawning period was reported to be limited to the months of September to March (Mimura, 1958; Kikawa, 1964a). Our study included fish from areas north of that traditionally fished by Japanese vessels, which may explain the extended spawning season. An increase in the length of the spawning season towards equatorial waters has been suggested for many species including black skipjack, *Euthynnus lineatus* (Schaefer, 1987), yellowfin tuna, *Thunnus albacares* (McPherson, 1991), blue marlin, *Makaira nigricans* (Hopper, 1990), and other multiple spawning fish (Qasim, 1955).

The actual duration of spawning in individual southern bluefin tuna could not be de-

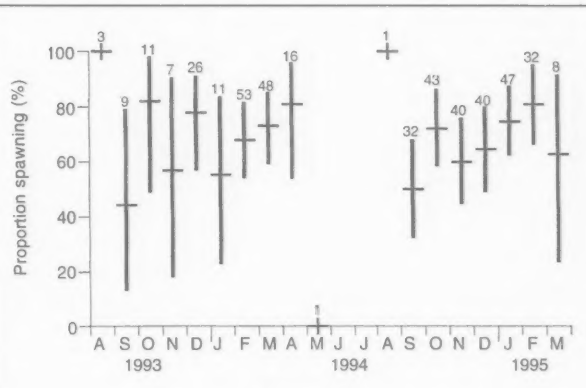

Figure 7

The proportion of southern bluefin tuna, *Thunnus maccoyii*, spawning by month. The vertical bars indicate 95% confidence limits of the mean for samples sizes >5. The numbers indicate sample sizes.

termined. However, the prevalence of females in different phases of spawning activity (nonspawning, spawning, or postspawning) on the spawning ground should be in direct proportion to the duration of that phase, if females in each phase are equally catchable. The ratio of nonspawners:spawners:postspawners for females caught on the spawning ground was estimated to be 0.30:0.69:0.01 or 0.44:1:0.01 if spawners are set as 1. In other words, spawning females were 2.3 times more prevalent than nonspawning females and 108 times more prevalent than postspawning females on the spawning ground. This finding indicates that the duration of the nonspawning phase is less than half, and the postspawning phase one onehundredth, of the duration of the spawning phase.

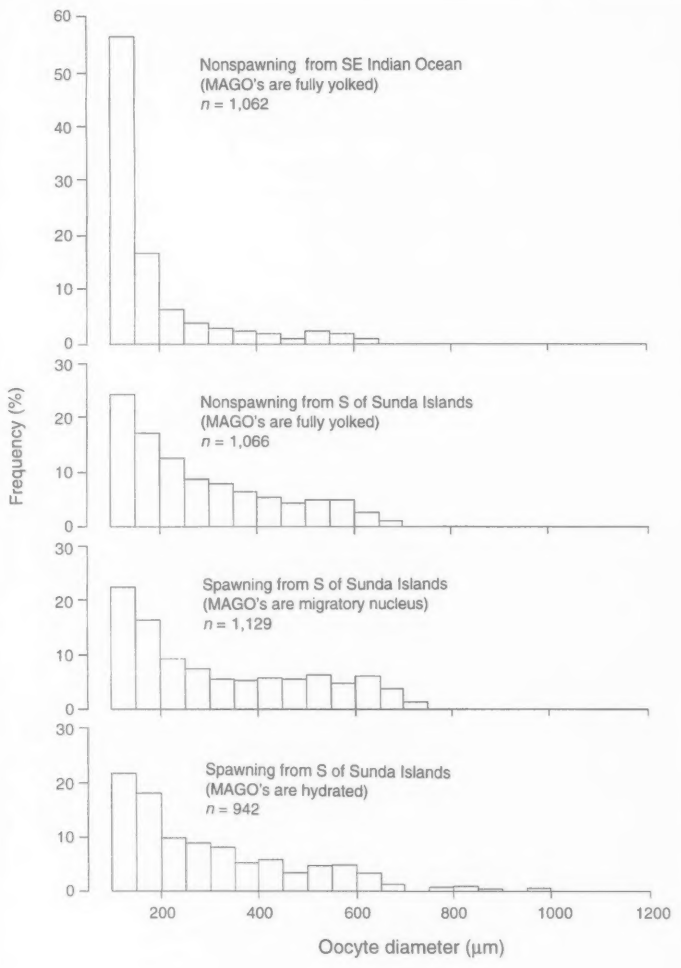

Figure 8

Size-frequency distribution of oocytes representing the advanced stages of maturation, by 50-µm intervals, in southern bluefin tuna, *Thunnus maccoyii*, ovaries. Only oocytes >100 µm were measured.

Spawning frequency and fecundity

The potential annual fecundity of southern bluefin tuna is indeterminate (not fixed prior to spawning) because unyolked oocytes are continually matured and spawned during the season. Annual fecundity is indeterminate in many tuna species such as black skipjack (Schaefer, 1987), skipjack tuna (Hunter et al., 1986), and yellowfin tuna (Schaefer, 1996). The fecundity of southern bluefin tuna was estimated by Kikawa (1964b) as the number of advanced yolked oocytes in the ovary, and by Thorogood (1986) as the number of oocytes >300 µm in diameter in the ovary. These estimations of fecundity were not potential annual fecundity because southern bluefin tuna are capable of continuously maturing and spawning oocytes from a pool of unyolked oocytes (<300 µm).

Southern bluefin tuna can spawn many times during a season. The ovaries of 25% of the females collected from the spawning ground contained evidence that they had all recently spawned (postovulatory follicles) and were about to do so again (migratory nucleus or hydrated oocytes). We assume that postovulatory follicles persist in the ovaries of southern bluefin tuna for about 24 hours as has been found in other tropical spawning tunas (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996). The average interval between spawning in southern bluefin tuna, estimated from the proportion of ovaries containing postovulatory follicles, was 1.1 days for females in "prime spawning condition." Similar spawning rates have been reported in other tuna species that spawn in tropical waters: 1.54 and 1.27 days for yellowfin tuna (McPherson, 1991; Schaefer, 1996); 1.1 days for bigeye tuna (Nikaido et al, 1991) and 1.18 days for skipjack tuna (Hunter et

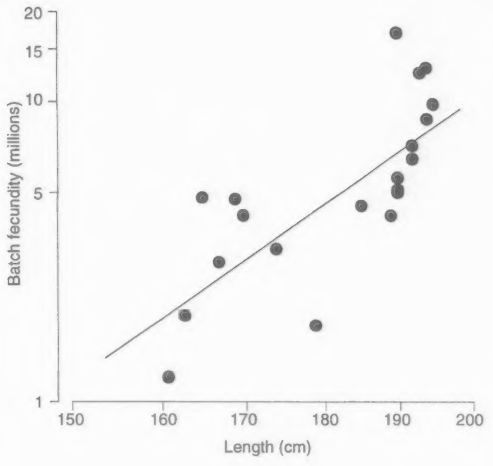

Figure 9

The relation between batch fecundity and length of southern bluefin tuna, *Thunnus maccoyii*, (both scales are logged).

al., 1986). The mean spawning interval of reproductively active yellowfin tuna (those whose ovaries contain advanced yolked oocytes and may or may not contain postovulatory follicles and contain no or less than 50% α atresia) was 1.14 days (Schaefer, 1996). Histological sections indicated that slight variations in the lengths of individual spawning intervals exist in southern bluefin tuna, which may be normal or the result of external stresses such as decreased food availability or the stress of capture (Hunter et al., 1986).

Our estimate of mean relative batch fecundity for southern bluefin tuna (57 oocytes per gram of body weight) is similar to that found in yellowfin tuna (68 oocytes per gram of body weight) (Schaefer, 1996) but less than that for black skipjack tuna (81 to 153 oocytes per gram of body weight) (Schaefer, 1987) and skipjack tuna (40 to 130 oocytes per gram of body weight) (Stéquert and Ramcharrum, 1995). Hunter et al. (1985) reported that the minimum number of females needed for a reliable batch fecundity estimate in northern anchovy was 50. We, however, found only 21 southern bluefin tuna ovaries with unovulated hydrated oocytes from the 475 ovaries collected from the spawning ground. There could be several reasons for this. Oocytes in the hydrated stage may be very short-lived in southern bluefin tuna, which would reduce the chance of sampling females with hydrated ovaries. Spawning may occur during a specific time of the day, and if sampling was not conducted just prior to this, fewer females with hydrated ovaries would be collected. Spawning in many tuna species is known to occur in the late evening or early morning (Hunter, et al., 1986; Schaefer, 1987; McPherson, 1991; Nikaido et al., 1991; Schaefer, 1996). Because our ovaries were sampled from females caught on Indonesian-based longlining vessels, which generally operate during daylight hours (Ishida et al., 1994), the chances of catching females that were about to spawn would be reduced. Further, if spontaneous spawning occurred while southern bluefin tuna were on the longlines, then fewer females with unovulated hydrated oocytes would be sampled. Spontaneous spawning has been observed in skipjack tuna soon after capture (Kaya et al., 1982).

Batch fecundity in southern bluefin tuna increased with body length. The variation in estimates for females of similar size may be normal because females were collected in different years and at different times in their spawning cycles. Hunter et al. (1985) suggested that the relation between batch fecundity and fish weight should be estimated annually in northern anchovy because batch fecundity can vary by a factor of 2 between years. Batch fecundity is also known to vary significantly during the spawning season in many fish species (Conover, 1985). A decrease in batch fecundity during the spawning season was found in Atlantic mackerel, *Scomber scombrus* (Watson et al., 1992), as individuals moved northwards. Batch fecundity can also peak during the middle of the spawning season if conditions are suitable, or it can remain constant if conditions are unpredictable (Conover, 1985).

Spawning strategies

We found that many southern bluefin tuna ovaries, collected both on and off the spawning ground, contained moderate levels of α atresia (10–50% of advanced yolked oocytes). High levels of α atresia are thought to indicate a decline in the spawning rate (Hunter and Macewicz, 1985a) and would normally occur towards the end of an individual's spawning season. Hunter and Macewicz (1980) classified northern anchovy as early postspawning if their ovaries contained less than 50% of advanced yolked oocytes in an α atretic state and postspawning if their ovaries contained more that 50% α atresia. Because we found that ovarian atresia increased with gonad index in the ovaries of prespawning females from the Southern Oceans, it appears that increased α atresia will not always mark the cessation of spawning in southern bluefin tuna. This ovarian atresia found in prespawning females could be a normal hormonal process that occurs during ovary maturation, as suggested by Macer (1974) for horse mackerel (*Trachurus*

trachurus). Atresia can also be caused by starvation as Scott (1962) found in maturing rainbow trout (*Salmo gairdneri*). It is not known if prespawning southern bluefin tuna are resorbing developing oocytes to gain the energy required for migration to the spawning grounds or because the ovary can only accommodate a certain volume of oocytes.

Many ovaries from nonspawning southern bluefin tuna ovaries collected from the spawning ground contained 10–50% atresia of their advanced yolked oocytes. The precise reproductive stage of these females is unclear. The similarity in atretic levels between these females and the prespawning females from the southern oceans, and in their high mean GI values, suggests that these females may have only just arrived on the spawning ground or were in the early stages of their spawning cycle. If this is the case, the relatively large numbers of nonspawning females (30% of females sampled) indicates that southern bluefin tuna may delay the onset of spawning possibly to recover from the energetic costs of migration. Their presence on the spawning ground throughout the spawning season suggests that there is a continual supply of new spawners onto the ground. Alternatively, southern bluefin tuna may not spawn continuously while on the spawning ground, but in pulses. The nonspawning females may be experiencing a lull in spawning activity between spawning episodes. The presence of many nonatretic yolked oocytes in their ovaries suggests that they could recommence spawning in the current season. Lunar spawning cycles have been documented in many tropical spawning fishes (see reviews by Johannes, 1978; Taylor, 1984; Robertson et al., 1990), however, we detected no evidence of a lunar cycle.

Spawning in southern bluefin tuna is not synchronized for the stock as a whole. There are several lines of evidence to support this statement: the presence of prespawning females both on and off the spawning ground throughout the spawning season; the absence of a peak in GI during the spawning season; the constant level of spawning intensity (percentage of females spawning) during the spawning season; the absence of any increase in the incidence of oocyte atresia towards the end of the spawning season; and the presence of postspawning females off the spawning ground both early and late in the spawning season. Thus it appears that there is a turnover of new spawners replacing old spawners on the spawning ground throughout the season. A similar turnover of pre- and postspawning southern bluefin tuna has been reported on the "Oki" fishing ground (Fig. 1) south of the spawning ground (Kikawa, 1964b). Nonsynchronized spawning has been found in other multiple spawning species such as skipjack tuna (Cayré and Farrugio, 1986), chub mackerel, *Scomber japonicus* (Dickerson et al., 1992), and Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994). Cayré and Farrugio (1986) reported that spawning in skipjack tuna in the Atlantic is synchronized within schools. Individuals in a school can mature rapidly and spawn batches of oocytes simultaneously when conditions become favourable. It is unclear if southern bluefin tuna can do this, or to what extent the long spawning season is the result of individual fish or schools arriving on the spawning ground and maturing at different times. It is also unclear if the spawning period is constant for all individuals. In many species, including jack mackerel, *Trachurus symmetricus*, and chub mackerel, *Scomber japonicus*, older spawners are reported to have a longer spawning period than younger spawners (Knaggs and Parrish, 1973; MacCall et al., 1980).

The low number of postspawning female southern bluefin tuna (3) found on the spawning ground suggests that as soon as individuals have finished spawning they quickly move off the ground. The reasons for this departure are uncertain, but it may be due to decreased food availability through increased competition because many fish are gathering to spawn in a relatively small area, or to an inability to withstand the warmer water temperatures on the spawning ground for extended periods of time. Adult bluefin tuna are unique among the tunas because they live predominantly in cold water (as low as 5°C) and only move into warmer waters to spawn (Olson, 1980). Their ability to maintain their body temperature above ambient water temperature, through the development of an increased lateral blood supply and heat exchangers, has enabled them to occupy higher latitudes than many tuna species can tolerate. This adaptation to cold water, however, may preclude them from extended stays in warm water, resulting in a rapid migration off the spawning ground after spawning.

After spawning, southern bluefin tuna migrate south from the spawning ground into the West Wind Drift (Mimura, 1962) to feed and gain condition over the southern winter months. The minimum time for an individual to travel to the Southern Ocean however, is unknown. The maximum sustained swimming speeds of small yellowfin and skipjack tunas are predicted to be between 2 and 4 body lengths/s (Brill, 1996), and these values are thought to be similar in other active fish species. Southern bluefin tuna are unlikely to travel at their maximum sustained swimming speed in a straight line from the spawning grounds to the southern oceans because they will be feeding on the way south. If a 180-cm fish travelled at between 1 and 2 body lengths/s, from the spawning ground to Tasmania (6,000 km), it would take

between 19 and 39 days. Warashina and Hisada (1970) reported that lean fish with brownish meat have been caught in the Tasman Sea as early in the spawning season as November. These lean fish are believed to be postspawning females who have recently migrated from the spawning ground. The earliest that postspawning females were observed on the spawning ground was in October of both the 1993–94 and 1994–95 spawning seasons. The appearance of these postspawning fish on the spawning ground in October and again around Tasmania in November supports the idea that southern bluefin tuna are capable of travelling that distance in approximately one month. It also supports the idea that individuals spawn for a relatively short time in contrast to the whole season.

Acknowledgments

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Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys

Paul C. Fiedler
Jay Barlow
Tim Gerrodette

Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038
E-mail address (for P. Fiedler): P.Fiedler@noaa.gov

Abstract.—Acoustic backscatter data from a 38-kHz echo sounder and a 150-kHz acoustic Doppler current profiler (ADCP) were collected during Southwest Fisheries Science Center marine mammal surveys in the eastern Pacific aboard the NOAA ship *David Starr Jordan* in 1992 and 1993. These data were processed to give profiles of volume scattering strength. A deep scattering layer dominated the time-depth patterns of backscatter. This layer migrated from a depth of 300–400 m during the day to 0–100 m at night, when it was located just above the thermocline. The source of backscatter was primarily small fish and squid, which are dolphin prey. Dolphin sighting rates were correlated positively with nighttime volume scattering strength above the thermocline. Spatial and temporal variability of prey biomass in the surface layer, as indexed by volume scattering strength, may have important consequences for dolphin feeding, as well as for distributional responses to habitat variability by dolphins.

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Acoustic data, consisting of the returns of pulses of sound from targets in the water column, are routinely used to assess fish distribution and abundance (Forbes and Nakken, 1972; Johannesson and Mitson, 1983; MacLennan and Simmonds, 1992). Such data are now also being used to quantify the biomass and distribution of zooplankton and micronekton (Greene and Wiebe, 1990; Hewitt and Demer, 1993). Innovative techniques using multifrequency amplitude and phase information can give estimates of size, movement, and acoustic properties of individual planktonic organisms (Farmer and Huston, 1988; Holliday et al., 1989). Another approach in acoustic studies of zooplankton and micronekton has been to employ instrumentation that is used routinely, notably the acoustic Doppler current profiler (ADCP, Roe and Griffiths, 1993). Several studies have used uncalibrated ADCP echo intensity data, with various levels of processing, to estimate relative patterns of plankton biomass distribution in space and time (Flagg and Smith, 1989; Plueddemann and Pinkel, 1989; Smith et al., 1989; Heywood et al., 1991).

We have been collecting echo intensity data from a 38-kHz echo sounder since 1986 and from a 150-kHz ADCP since 1992 on Southwest Fisheries Science Center marine mammal surveys. This report describes data collection and processing and presents results from two cruises during which nearly complete data sets were obtained (population of *Delphinus* stocks 1992 [PODS92] and 1993 [PODS93]) (Fig. 1). Other data collected on these surveys provide a context for these results in terms of predators and habitat. Line-transect data were collected for dolphin abundance estimates (Mangels and Gerrodette, 1994a, 1994b). We use sighting rate here as an index of dolphin abundance. Physical and biological oceanographic data were also collected to characterize habitat variability (Philbrick et al., 1993).

Materials and methods

A 38-kHz Simrad EK-400 scientific sounder was used on NOAA ship *David Starr Jordan* beginning in 1986. Rather than a commercial echo integrator, we used an acoustic data acquisition (ADA) system, consisting of an analog-to-digital converter and a personal computer. A 150-kHz ADCP was installed on the *Jordan* in 1991. We collected nearly complete sets of 38- and 150-kHz acoustic data in 1992 and 1993.

A sonar equation relating volume backscattering strength per m^3 (S_v,

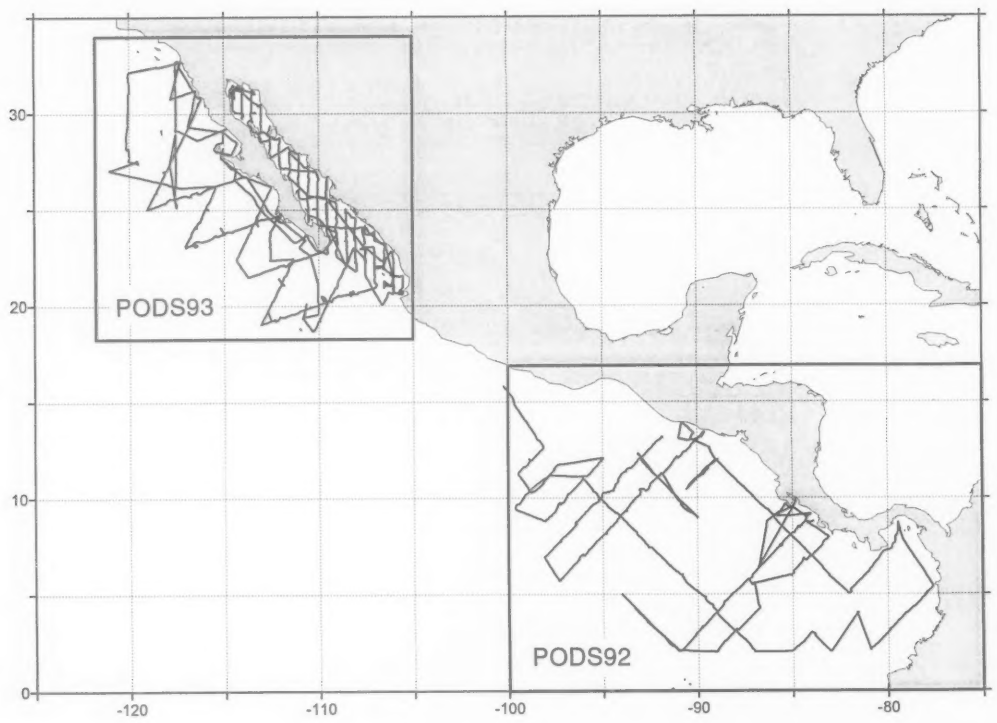

Figure 1

Cruise tracks of NOAA ship *David Starr Jordan* during Population of *Delphinus* Stocks (PODS) cruises (28 July–2 November 1992) and (28 July–6 November 1993).

dB // 1μ*Pa* at 1 m) to the echo level (EL), integrated and recorded after 20logR TVG amplification in the transceiver, was formulated as follows (Simmonds, 1990):

$$S_v = EL - (SL + RR) - 10 \log \psi - 10 \log c\tau/2, \quad (1)$$

where EL = 20 log V_o (dB) (V_o="gain-controlled envelope" signal, volts);
SL = source level (dB);
RR = receiver response (including receiver gain and transducer on-axis voltage response), dB;
10 log ψ = equivalent beam angle;
c = speed of sound (m/s);
τ = pulse length (1 × 1/1,000 per millisecond).

Transmission loss does not appear in this equation because it was corrected by a 20log$R$ time-varied gain (TVG) function applied to V_o in the transceiver. The TVG was checked with a transceiver test mode that input a constant voltage signal. The recorded 20log$R$ TVG output did not differ significantly from the theoretical function ($TVG = 20 \log R + 2\alpha R$, where α is the nominal sound absorption coefficient of 0.008 dB/m and R is range in meters). The range (R) was based on a sound velocity entered into the control unit at the start of the cruise.

On-axis sensitivity (SL+RR) was estimated by measuring the system response (EL) to a standard calibration sphere (38.1-mm diameter tungsten carbide with 6% cobalt binder, target strength TS = –42.3 dB; Foote, 1990) suspended 7 m below the transducer. In this case, Equation 1 reduces to

$$EL = TS + (SL + RR), \quad (2)$$

where $EL = 20 \log V_o + 20 \log R$.

The "gain-controlled envelope" signal (V_o) represents a peak voltage and was converted to a root-mean-square (rms) voltage by multiplying by $1/\sqrt{2}$. The additional 20log$R$ term was added to the system's 20logR TVG, used during the echo-integration surveys, to correct for the spherical spreading of the return from the point calibration target. Solving Equa-

tion 2 for the on-axis sensitivity gave ($SL+RR$) = 74.2 dB.

Operationally, the ADA program squared V_o, which is proportional to pressure at the face of the transducer, to give an echo intensity value (Eq. 1) proportional to power or energy flux per unit of area. The intensity values were then binned in 50 10-m bins between 10-m and 510-m depth. The binned intensities were averaged at 10-sec intervals over ten minutes (60 pings), equivalent to an interval of 3 km at the typical ship speed of 18 km/h. Recorded intensities were converted to units of decibels (dB=10 log I/I_r, where I_r represents the standard reference of 1μPa at a 1-m distance from the face of the transducer). Then, a correction to the TVG function was formulated by using depth-dependent sound velocities and attenuation coefficients calculated from CTD data taken once or twice daily with the algorithms of Francois and Garrison (1982). Finally, a constant 53.4 dB was subtracted to account for the combined source level, transducer response, receiver gain, and beam pattern terms ($-SL - RR - 10 \log \psi - 10 \log \tau/2$) in Equation 1. The equivalent beam angle is very difficult to measure directly without special apparatus; therefore we used the manufacturer's nominal value (10 log ψ=–19.6 dB; Simrad EK400 Scientific Sounder Instruction Manual).

Acoustic Doppler current profilers have been used since the early 1980's to estimate current velocity from the Doppler shift of acoustic signals backscattered from suspended matter (plankton and sediments) in the water column. Echo intensity is calculated and recorded during data-processing. RD Instruments has developed instrument modifications and an algorithm to calibrate these values and to estimate volume backscattering strength (S_v, dB). The algorithm is based on the following working version of a sonar equation (RD Instruments, 1990):

$$S_v = 10 \log \left[\begin{array}{c} 4.47 \times 10^{-20} K_2 K_s (T_t + 273) \\ \left(10^{k(E-E_r)/10} - 1\right) R^2 / \\ \left(c P K_1 10^{-2\alpha R/10}\right) \end{array} \right], \quad (3)$$

where K_2 = system noise factor = 4.3;
K_s = system constant = 4.17×10^5;
T_t = transducer temperature (°C);
k = conversion factor = 0.435 dB/count;
E = echo intensity (counts);
E_r = reference level for echo intensity (counts);
R = slant range (m);
c = sound velocity (m/s);
P = transmit pulse length = 8 m;
K_1 = power into the water, W;
α = sound absorption coefficient (dB/m).

Although this equation was formulated to be applied to individual beams of the ADCP, we used average amplitude data for E because we were using an empirical reference level (E_r). The reference level for echo intensity, E_r, represents thermal noise in the system electronics plus ship noise. E_r was assumed equal to the minimum value of E (<40 counts) observed in each average profile or ensemble (~740 pings in 10 minutes). The manufacturer states that this in-situ method of estimating E_r is preferable to calculating E_r from measured system temperatures. Because ship temperature was relatively constant and water temperature ranged over only 4°C in 1992 and 10°C in 1993, E_r varied by only (±7–8 counts. Values of E < 10 counts were not used (RD Instruments, 1990) and appear as blank areas at depth in 150 kHz time-depth sections (Fig. 2).

Values for c and α were calculated from CTD data taken once or twice daily according to Francois and Garrison (1982). Transducer temperature, T_t, was assumed equal to observed surface temperature. Slant range, R, was corrected for estimated sound velocity in relation to the value assumed by the ADCP software (1,475 m/s). The conversion factor, k (dB/count), depends on the temperature of the system electronics. However, the deck unit was located in a temperature-controlled room (18–21°C) so that the range of k was 0.433 to 0.437 (<1 dB). Power into the water, K_1, was assumed constant and estimated to be 53.4 W (RD Instruments, 1990). The ADCP was set up with 50 bins of length 8 m, starting at 4 m from the transducers.

In both the 38- and 150-kHz data sets, the depth bin representing the bottom was identified initially by an algorithm searching for strong gradients of $S_v(z)$. These results were modified by visual inspection of time-depth sections. Data from the bottom depth bin and below were excluded from subsequent analysis. Some 1992 and 1993 profiles of S_v appeared to be biased low on account of sound attenuation due to bubbles beneath the ship during stationkeeping and during very rough weather (cf. Fig. 2, 20 August, at the first tick marking the morning CTD station). We identified biased profiles from anomalously low S_v in bins below the top depth bin. The problem was more prevalent in the 150-kHz data (2.5% of 1992 profiles and 1.0% of 1993 profiles) than in the 38-kHz data (0.5% of 1992 profiles and 0.1% of 1993 profiles). We excluded the biased profiles from statistical analyses.

Dolphin sightings were recorded during daylight hours from the flying bridge of the vessel by a team

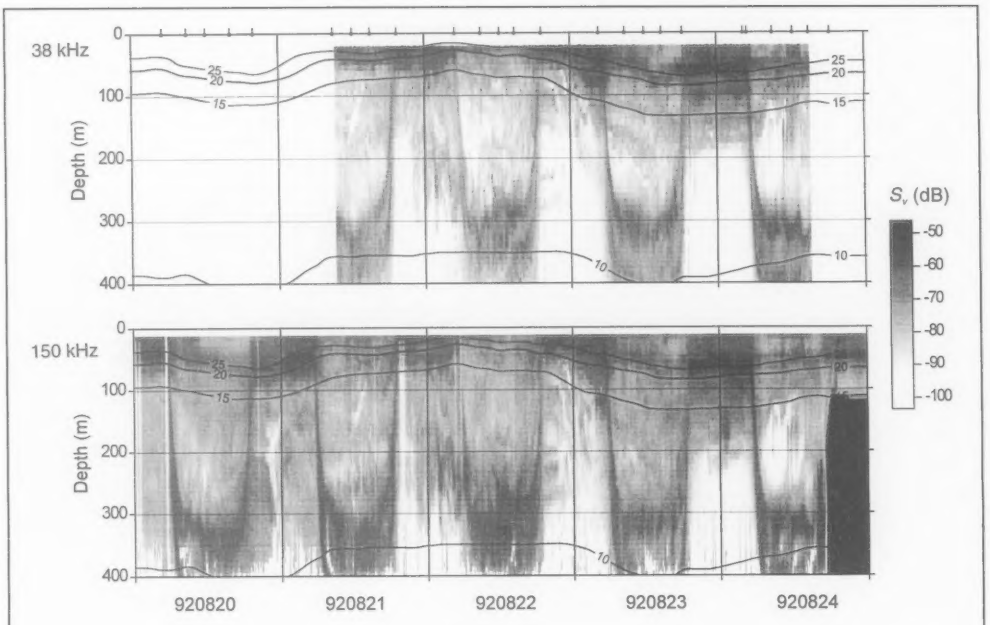

Figure 2

Time-depth sections of 38-kHz and 150-kHz volume scattering strength (S_v, dB) and temperature during five days of PODS92 surveys. Contour lines are isotherms (°C), from XBT (expendable bathythermograph) profiles at tick marks along top of section.

of three observers using 25-power binoculars (Mangels and Gerrodette, 1994a, 1994b). Local dolphin abundance was indexed by the number of sightings of spotted (*Stenella attenuata*), spinner (*S. longirostris*), striped (*S. coeruleoalba*), common (*Delphinus delphis* and *D. capensis*), bottlenose (*Tursiops truncatus*), Risso's (*Grampus griseus*), rough-toothed (*Steno bredanensis*), Fraser's (*Lagenodelphis hosei*), Pacific white-sided (*Lagenorhynchus obliquidens*), and unidentified dolphins. Daily numbers of sightings were standardized to sighting rates of schools or individuals per 100 km in optimum sea-state conditions (Gerrodette[1]). Sighting rates were log-transformed to normalize distributions before testing correlation with various time and depth means of $S_v(z,t)$. We report correlations with 150 kHz $\overline{S}_v$ here because data were collected on about 25% more days than those for 38kHz $\overline{S}_v$.

Acoustic and other data were gridded by kriging with the software SURFER (Golden Software, 1995). Variogram models were fitted to the data and the best fit was selected by using the original code based on Pannatier (1996). Contour maps were also generated with SURFER .

Results

The five-day time-depth sections in Figure 2 illustrate features observed in all sections: 1) data at one or both frequencies were occasionally missing; 2) the 150-kHz signal was lost in the noise at depths >200 m; and 3) bottom depth was <400 m as on 24 August after about 1700 hours. All time-depth sections of S_v were dominated by a deep-scattering layer (DSL) at 300–400 m depth during daylight hours and 0–100 m during the night. The DSL migrated about 200 m in 1–2 hours near dawn and dusk. Morning descent was generally more rapid than evening ascent. During some days, the DSL was split into two distinct layers at depth, separated by up to 100 m (cf. Fig. 2, 38 kHz section on 22 and 23 August).

The DSL was detected at both 38 and 150 kHz. However, the 150-kHz return from the DSL at its daytime depth was barely above background noise levels. The smaller effective depth range of the ADCP was due to 1) greater attenuation of sound at the higher frequency (α=0.039 dB/m at 150 kHz com-

[1] Gerrodette, T. 1996. On estimating relative abundance. Unpubl. manuscript.

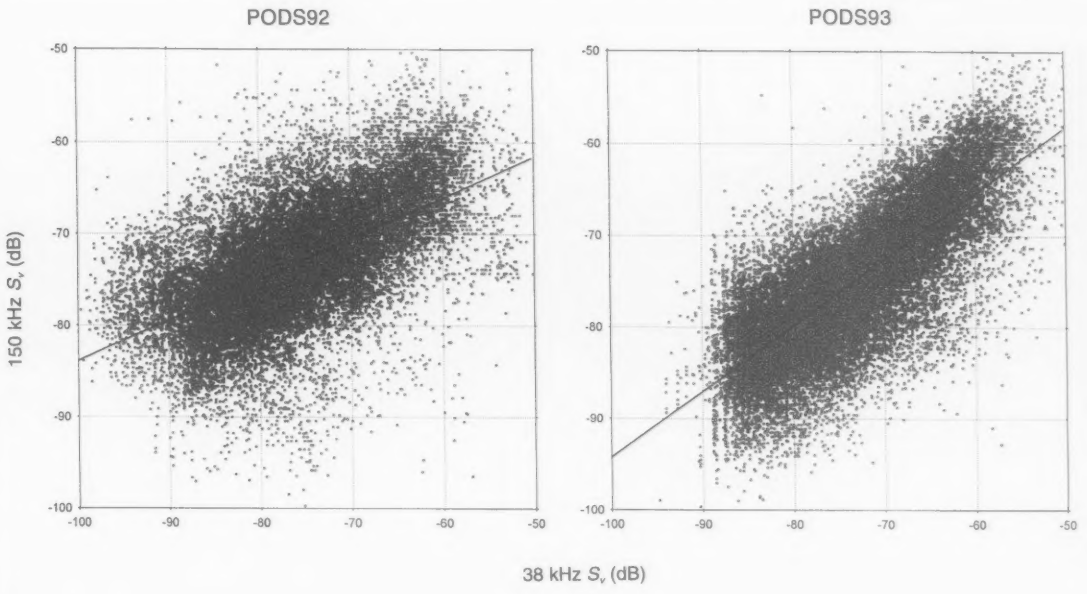

Figure 3

Relationships between 38-kHz and 150-kHz volume scattering strength (S_v, dB) in corresponding 10-and 8-m depth bins (centered at 25, 65, 105, 145, 185, 225, 265, and 305 m) at all times of day or night during PODS92 (n=24,193) and PODS93 (n=26,963) surveys.

pared with 0.008 dB/m at 38 kHz) and 2) transducer orientation 30° off the vertical, resulting in a slant range 15% greater than depth.

Volume scattering strengths at 38 and 150 kHz were significantly correlated (Fig. 3, r=0.58 in 1992 and r=0.77 in 1993). Some error in this relation is due to the different sizes and inexact depth matching of bins between frequencies. The ADCP samples echo intensity only in the last quarter of each depth bin, so that scattering is averaged over only 2 m, compared with 10 m for the 38-kHz echo sounder. Correlation decreased at depth (e.g. in 1993, r=0.83 at 25 m and r=0.53 at 185 m). This could have been due simply to the low signal to noise ratio at depth in the 150-kHz data. However, it probably also reflects changes in species and size composition, and thus spectral response, of scatterers at depth. The mean difference between 38- and 150-kHz volume scattering strength in Figure 3 was –2.9 dB in 1992 and 0.0 dB in 1993.

Spatial patterns of mean day and night volume scattering strength ($\overline{S}_v$) in the surface layer (0–100 m) were very similar at the two frequencies; therefore only the 38-kHz patterns are illustrated here (Figs. 4 and 5). On average, night values exceeded day values by 6.4 dB in 1992 and 11.0 dB in 1993 (Table 1). Thus, near-surface $\overline{S}_v$ was 4 and 13 times greater at night than during the day, indicating that 77–92% of the scatterers left the surface layer during the day. Mean surface $\overline{S}_v$ values (daily or nightly, 38 or 150 kHz) varied by 11.5 to 20.6 dB during the cruises, representing ranges of 14 to 115 times.

In 1992, low $\overline{S}_v$ was observed along 8–9°N both night and day (Fig. 4). $\overline{S}_v$ increased to the south towards the equator and to the north and east towards

Table 1

Mean day (0800–1600) and night (2000–0400) volume scattering strengths (S_v,dB) in the surface layer (0–100 m) in 1992 and 1993. Values are cruise means, with range in parentheses. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

		Day	Night
PODS92	38 kHz	–75.1 (–82.2 to –70.7)	–68.6 (–77.1 to –62.0)
	150 kHz	–73.9 (–83.7 to –69.0)	–67.5 (–76.8 to –57.3)
PODS93	38 kHz	–76.3 (–85.8 to –69.4)	–65.3 (–73.5 to –60.2)
	150 kHz	–79.2 (–90.2 to –70.1)	–68.2 (–80.3 to –59.7)

the coast. The highest $\overline{S}_v$ values were observed along the coast of Costa Rica and the coast of Mexico south of the Gulf of Tehuantepec (16°N, 95°W).

In 1993, $\overline{S}_v$ was high in the Gulf of California and along the Pacific coast of southern Baja California (Fig. 5). $\overline{S}_v$ was generally low in the northern and

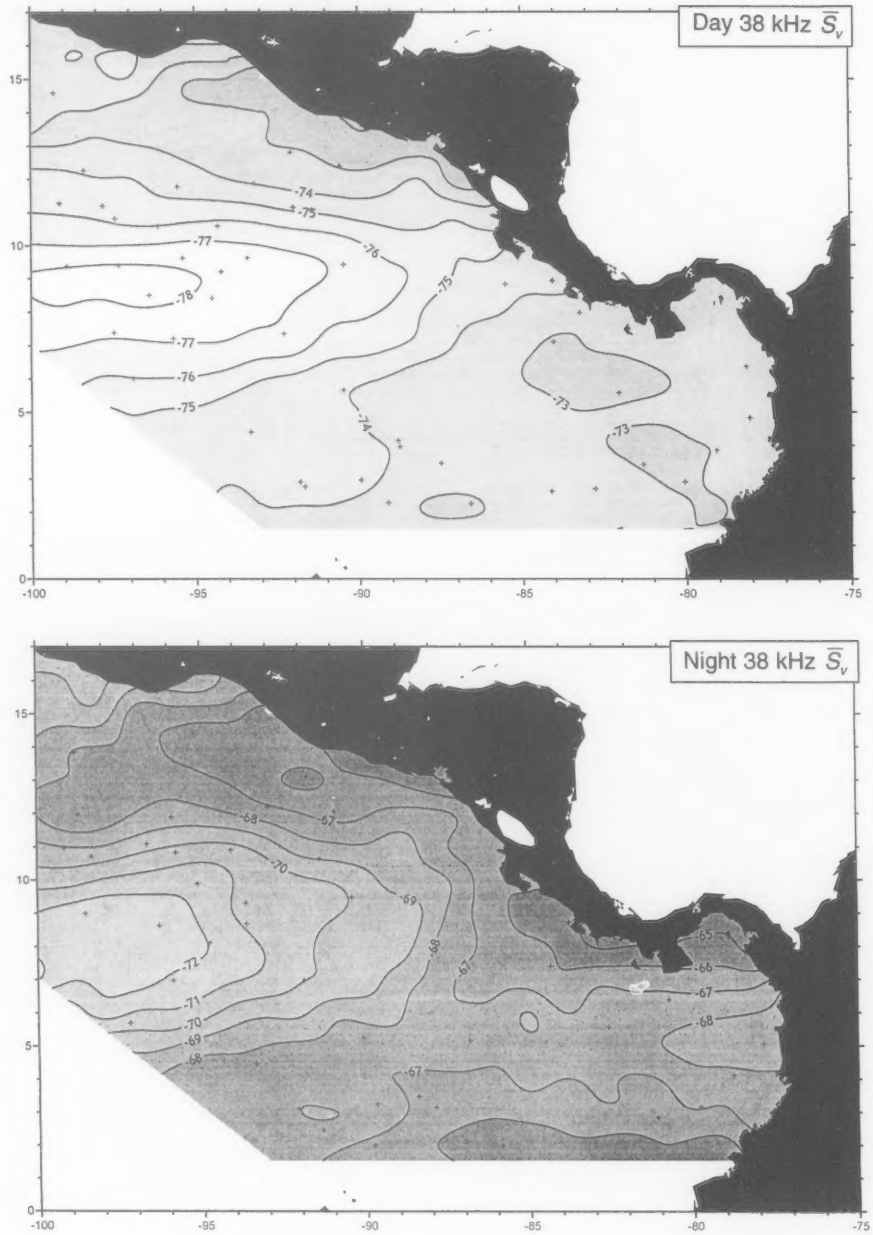

Figure 4

Maps of daily (0800–1600) and nightly (2000–0400) 38-kHz mean volume scattering strength (S_v, dB) in the surface layer (0–100 m) during PODS92 surveys, 28 July –2 November 1992.

offshore part of the study area and increased towards the southeast corner near Cabo Corrientes (20°N, 105°W).

Time-depth sections (Fig. 2) show a close relation between the deep scattering layer and the thermocline at night. The DSL ascended through the thermocline in the evening, then remained just above the thermocline until it descended in the early morning. The DSL followed changes in the depth of the thermocline during some nights (cf. 22–23 August, Fig. 2). Where the thermocline is deep, S_v is maximum at 10–20 m above the thermocline and then declines closer to the surface. Where the thermocline is shallow, S_v is maximum at, or very close to, the surface. The nighttime depth of the DSL was significantly correlated with thermocline depth, except for the 38-kHz DSL in 1993 (Table 2). Mean $\overline{S}_v$ above the thermocline was slightly, but not significantly, greater above more shallow thermoclines 1992.

Dolphin abundance, as indexed by sighting rates of schools or individuals per 100 km, was significantly correlated with nighttime mean $\overline{S}_v$ above the thermocline in 1992 and with 0–400 m mean $\overline{S}_v$ in 1993 (Table 3, the 150-kHz results are shown here owing to larger sample sizes but the 38-kHz results were similar). In 1992, both mean $\overline{S}_v$ above the thermocline and dolphin abundance were high near the countercurrent thermocline ridge along 9°N (Fig. 6). In 1993, mean $\overline{S}_v$ above the thermocline and dolphin abundance were relatively high near the mouth of the Gulf of California, at intermediate thermocline depths.

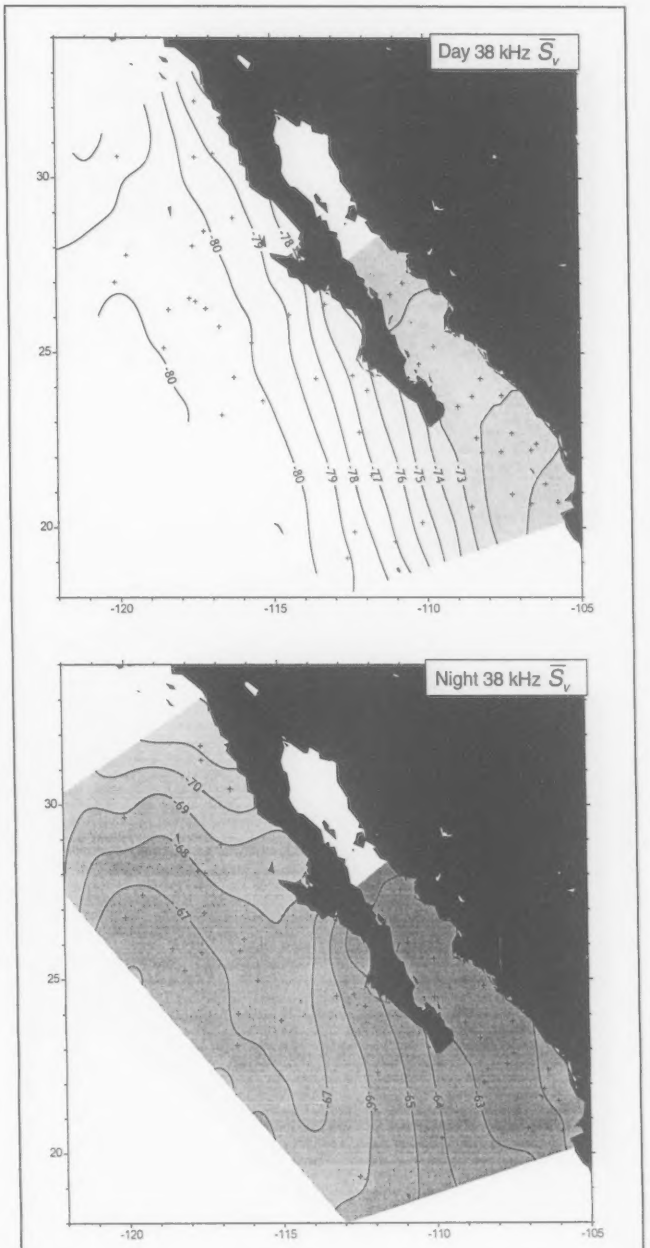

Figure 5

Maps of daily (0800–1600) and nightly (2000–0400) 38-kHz mean volume scattering strength (S_v, dB) in the surface layer (0–100 m) during the PODS93 survey, 28 July–6 November 1993.

Discussion

Deep scattering layers have been observed throughout the Pacific with low-frequency depth sounders (<30 kHz). Tont (1976) reported mean daytime depths of 319 m in the eastern tropical Pacific and 282 m in the California Current, similar to the depths observed here (Fig. 2). Small mesopelagic fish with gas-filled swimbladders are now recognized to be the most important low-frequency backscatterers in the open ocean (Chapman, 1947; Marshall, 1951; Brooks, 1977), although early reports attributed DSL's to cephalopods (Lyman, 1948) or euphausiids (Hersey and Moore, 1948).

What do our acoustic observations represent? Volume scattering strength (dB) represents a sum of individual target strengths (TS), except at very high target densities where shadowing and multiple scat-

tering occur (MacLennan and Simmonds, 1992). Target strength is a nonlinear function of sound frequency and the cross-sectional area of the target (Demer and Martin, 1995) and TS per unit of area is typically expressed as a function of the dimensionless number (ka), where k is the acoustic wavenumber ($k=2\pi/\lambda$) and a is a characteristic dimension of the target (Chu et al., 1992). At low sound frequencies ($ka<1$, "Rayleigh" scattering), TS drops off rapidly. Thus, scattering of relatively low frequency sound by small targets is weak. At high frequencies ($ka>1$, "geometric" scattering), early models predicted TS to be approximately constant (Love, 1977). Most other models of geometric scattering are highly nonlinear, with deep nulls in individual TS versus (ka) curves. However, Chu et al. (1992) suggested that averaging over pings and individuals in field studies of volume backscattering should "smear out" these nonlinearities.

The wavelengths of 38-and 150-kHz sound correspond to target dimensions of approximately 4 and 1 cm, respectively. This is the effective size of macrozooplankton and micronekton organisms, such as euphausiids, siphonophores, small fish, and squid. Targets <4 cm, such as copepods, will scatter sound strongly at 150 kHz. Scattering of 38-kHz sound will be relatively weak Rayleigh scattering and may be undetectable over system noise. These smaller targets may have weakened the correlation between backscattering at the two frequencies (Fig. 3).

We were unable to make net tows to identify acoustic targets, owing to time constraints on the cetacean survey cruises. Therefore, we can make only an educated guess about the composition of the observed deep-scattering layers. Roe et al. (1984), in a uniquely comprehensive study of a community of vertically migrating organisms in the temperate northeast Atlantic, considered fish, decapod crustaceans, mysids, euphausiids, amphipods, copepods, ostracods, siphonophores, medusae, ctenophores, and chaetognaths. Ignoring small or weak scatterers, we must consider fish, crustaceans (decapods, mysids, and euphausiids), and siphonophores, as well as cephalopods, as possible components of the observed DSL's.

Average biomass densities of mesopelagic fish (primarily myctophids) and cephalopods are equal to, or slightly greater than, those of crustaceans in the eastern tropical Pacific (Blackburn, 1968; Blackburn et al., 1970) and subtropical Pacific (Maynard et al., 1975). Target strength depends on the composition, shape, and orientation of the target, as well as on relative size. At 38–120 kHz, small fish with gas-filled swim bladders (e.g. clupeoids) and squid have target strengths 5–10 dB greater than those for crustaceans of the same size (Tables 6.3 and 6.4 in MacLennan and Simmonds, 1992; Marchal et al., 1993). Siphonophores have a gas bladder that scatters sound and have been observed migrating with myctophids in a DSL off Baja California (Barham, 1966). However, myctophids, flying fish, and squid were much more abundant than siphonophores at night dipnet stations on our cruises.[2] Therefore, mesopelagic fish and

Table 2

Pearson product-moment correlations between properties of the nighttime (2000–0400) deep-scattering layer and the thermocline depth observed in 1992 and 1993. S_v = volume scattering strength (dB). Thermocline depth = depth of maximum 10-m temperature gradient. ***=$P<0.001$, **=$P<0.01$. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

		Correlations with thermocline depth	
		Depth of maximum S_v	Mean S_v above thermocline
PODS92	38 kHz	+0.86***	–0.15
	150 kHz	+0.84***	–0.23
PODS93	38 kHz	+0.25	–0.01
	150 kHz	+0.43**	+0.15

Table 3

Correlations between dolphin sighting rates (schools and individuals per 100 nautical miles of effort, log-transformed) and mean 150-kHz volume scattering strength (S_v, dB) above the thermocline at night (2000–0400), and 0 to 400 m night and day (0800–1600). *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

	Dolphin sighting rates	
	Schools	Individuals
PODS92		
Night S_v above thermocline	+0.35*	+0.38**
Night S_v 0–400m	+0.05	+0.02
Day S_v 0–400m	–0.01	–0.02
PODS93		
Night S_v above thermocline	+0.27	+0.15
Night S_v 0–400m	+0.36**	+0.20
Day S_v 0–400m	+0.38**	+0.18

[2] Pitman, R. 1996. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Box 271, La Jolla, CA 92038. Personal commun.

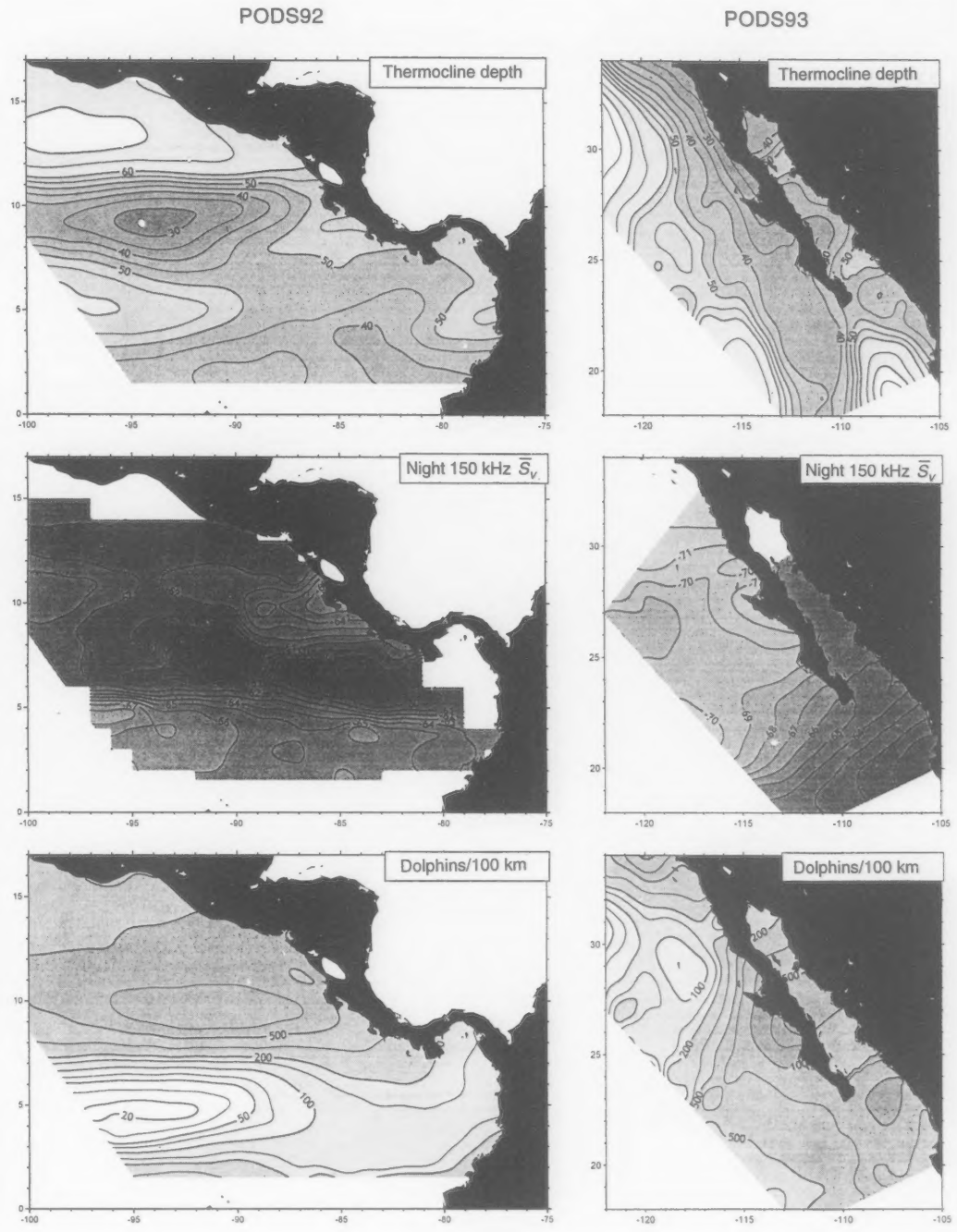

Figure 6

Thermocline depth (m), average nighttime backscatter above the thermocline (dB), and dolphin sighting rate observed in 1992 and 1993.

squid were most likely the major component of the observed DSL's, although a variety of crustaceans were undoubtedly present in the survey areas. Nonmigrating, epipelagic fish and squid are likely represented by near-surface backscattering during the day.

The small fish and squid that we argue were detected by our acoustic systems are dolphin prey (Fitch and Brownell, 1968; Miyazaki et al., 1973; Perrin et al., 1973; Robison and Craddock, 1983; Robertson and Chivers, 1997). The ranges of volume scattering strength we observed—more than three orders of magnitude among bins (Fig. 2), up to 10× variation between night and day and 500× variation among daily means—must be important factors in dolphin feeding strategies and habitat choices. Thermocline depth, which influences prey distribution, is an important component in dolphin habitat variability (Reilly and Fiedler, 1994).

We observed a positive correlation between the abundance of dolphins (observed during daylight) and the abundance of prey at night, when spotted and spinner dolphins are known to feed on mesopelagic prey near the surface (Perrin et al., 1973; Robertson and Chivers, 1997). Over 90% of the dolphins identified in both surveys were common, spotted, spinner, and striped dolphins. In the eastern tropical Pacific (PODS92), a region characterized by a strong and shallow thermocline (Wyrtki, 1967), nighttime prey abundance was more closely related to thermocline depth. Off Baja California (PODS93), the thermocline had less influence on distribution of prey. Dolphin community structure was also different: common dolphins represented 61% of the identified dolphins in this region, compared with only 37% in the PODS92 survey area.

Our results indicate that dolphin distribution can be related to prey abundance measured acoustically and that the physical environment influences the abundance of dolphin prey. Marchal et al. (1993) observed a similar DSL in the eastern tropical Atlantic that was related both to thermal structure and to tuna abundance. Simple and readily available sonar systems can yield useful results when survey time or resources are limited. Monitoring long-term changes in zooplankton or micronekton biomass, as Roemmich and McGowan (1995) did with net samples off southern California, could be facilitated by the application of such acoustic methods. However, in present and future studies of cetacean feeding and cetacean responses to habitat variability, we will use multispectral acoustic systems and validation by net samples to quantify availability and distribution of specific prey types.

Acknowledgments

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Feeding habits of pelagic summer flounder, *Paralichthys dentatus*, larvae in oceanic and estuarine habitats

Jill J. Grover
College of Oceanic and Atmospheric Sciences
Hatfield Marine Science Center
Oregon State University
Newport, Oregon 97365
E-mail address: jj.grover@hmsc.orst.edu

Abstract.—Pelagic larval summer flounder, *Paralichthys dentatus*, were collected in the NW Atlantic Ocean from 1985 to 1993, and their feeding habits were examined in relation to larval stage. Collections included preflexion, flexion, premetamorphic, and metamorphic larvae, although preflexion larvae composed the bulk of the specimens. Incidence of feeding and gut-fullness data indicated that larvae began feeding near sunrise and continued feeding throughout daylight hours. Incidence of feeding reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.6% at 0600–0759. Maximum gut fullness was seen between 1200 and 1559. The only time during which all larvae contained prey in their guts was 0800–0959. Immature copepodites were the primary prey for all oceanic larval stages. In addition, small prey, such as tintinnids and copepod nauplii, made major contributions to the preflexion diet, and large prey, such as calanoid copepods and appendicularians, made major contributions to the diets of premetamorphic and metamorphic larvae. Metamorphic larvae were also collected as they entered a New Jersey estuary, at night, and their diet was examined. At 1800–1959 and 2000–2159 hours, the incidence of feeding in estuarine larvae was significantly lower than in oceanic larvae. The estuarine diet was dominated by the calanoid copepod, *Temora longicornis*. Incidence of feeding was observed to decline as metamorphosis progressed, from 19.1% at stage G to 2.9% at stage H. However, this apparent cessation in feeding, when the right eye was at the midpoint of migration, may not bring about undue ecological peril to summer flounder larvae.

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The summer flounder, *Paralichthys dentatus*, an important component of recreational and commercial fisheries over the continental shelf and in estuaries of the Middle Atlantic Bight (United States), is currently overexploited. Evidence of this includes a drastic reduction in both commercial and recreational landings, in relation to peak years, and compressed age structure (Able and Kaiser, 1994). Both the fishery's decline and efforts to culture summer flounder (Bengtson et al., 1994; Bengtson and Nardi, 1995) are reviving interest in the basic biology of this species. Although much is known about the early life history of summer flounder, beginning with a description of eggs and larvae (Smith and Fahay, 1970) and including the timing of spawning, offshore distribution of eggs and larvae (Smith, 1973; Able et al., 1990), inshore occurrence of larvae and juveniles (Able et al., 1990), patterns of metamorphosis (Keefe and Able, 1993), and settlement processes (Burke et al., 1991; Keefe and Able, 1994; Norcross and Wyanski, 1994), many gaps still exist in our collective knowledge of larval and early-juvenile ecology.

Because survival beyond the early life history stages is based on an "eat and not be eaten" strategy (Keenleyside, 1979; Olla and Davis, 1988; Olla et al., 1994), feeding habits clearly define much of larval and early-juvenile ecology. Recently, larval summer flounder studies have focused on the effects of delayed feeding on survival and growth (Bisbal and Bengtson, 1995a), describing the starving condition (Bisbal and Bengtson, 1995b) and the development of the digestive tract (Bisbal and Bengtson, 1995c). Although these studies examined natural rates and processes, they were all conducted on larvae that were reared in a laboratory. Most of what is known about the early feeding ecology of wild summer flounder has been derived from metamorphosing larvae and early juveniles that were captured with benthic trawls in estuarine nursery habitats (Burke, 1995). Beyond the patent inference that planktonic larvae ingest plankton (e.g. Morse, 1981), very little is known regarding the early pelagic feeding ecology of this species (Rogers and Van Den Avyle, 1983; Grimes et al., 1989).

This study considers feeding ecology of larval summer flounder collected in pelagic habitats in the NW Atlantic Ocean from 1985 to 1993. Feeding habits were examined in relation to larval stage. Metamorphic larvae were also collected as they entered an estuarine habitat in New Jersey, and their diet was examined.

Materials and methods

During fall and winter, pelagic larval summer flounder were collected in the NW Atlantic Ocean from 1985 to 1993 by the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys (Able et. al., 1990). These monthly to bimonthly surveys were conducted over the continental shelf from Cape Lookout, North Carolina, to Cape Sable, Nova Scotia, by the RV *Albatross IV* and the RV *Delaware II*. The vast majority (96.4%) of oceanic specimens were collected during October and November, and a few were collected in December, January, and March. Surveys used 61-cm diameter bongo frames fitted with 0.333- and 0.505-mm mesh nets (Sherman, 1980). The nets were towed obliquely through the water from the surface to depths of 22–75 m and back to the surface at a speed between 1.5 and 3.5 knots. Samples from 50 stations were the focus of this study (Fig. 1). Collections were chosen for analysis on the basis of number of summer flounder larvae that were present. All collections with 10 or more summer flounder larvae were examined. Additional stations with fewer specimens were examined to balance time blocks so that each 2-h block included at least 10 specimens and at least 2 collections, and to include the full size range of larvae.

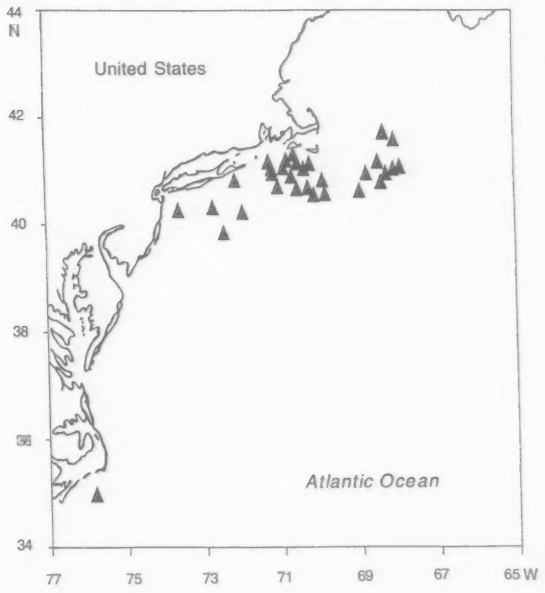

Figure 1

Location of the oceanic sites in the NW Atlantic Ocean, off the NE United States, where pelagic larval summer flounder, *P. dentatus*, were collected.

Specimens were preserved in 10% formalin at sea and remained in formalin for approximately 12 months. They were then transferred to 70% ethanol. Specimen shrinkage clearly occurred as a result of fixation. Within 24 hours of examination specimens were soaked in glycerin where they remained throughout their dissection (see Arthur, 1976; Gadomski and Boehlert, 1984).

After standard length (SL) (snout to notochord tip until full flexion, then to posterior edge of hypurals, Gadomski and Boehlert, 1984) of each larva was measured and morphological stage was determined, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified to the lowest possible taxon.

Diet was analyzed in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), and percent frequency of occurrence (%FO). Prey that comprised <1% of the diet by number and by volume were pooled into the "other" prey category. Prey volumes were estimated, generally by assuming a spheroidical geometry, from prey dimensions. The three analyses (%N, %Vol, and %FO) were combined to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI = (%N + %Vol) × %FO) (Pinkas et al., 1971).

A comparison of larval sizes with established definitions of length at yolk absorption and length at flexion (Smith and Fahay, 1970; Martin and Drewry, 1978) revealed that considerable shrinkage had occurred prior to the examination of these specimens. As a result, data were pooled across stations for analysis by morphological stage, rather than by size class. Morphological stages were defined as preflexion (PF): straight notochord and no indication of caudal-fin ray development; flexion (FLX): beginning of caudal-fin ray development (i.e. ossification), accompanied or not by an upturn of the notochord tip and ossification of ural bones (hypurals, epurals, parahypurals); postflexion, premetamorph (PM): completion of caudal-fin ray ossification, upturn of notochord, and ossification of the ural bones, accompanied by resorption of the notochord tip, such that it no longer extends beyond the edge of the hypural bones (Fahay[1]); and metamorph (M): metamorphic

[1] Fahay, M. 1995. Northeast Fisheries Science Center, Howard Marine Sciences Laboratory, Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732. Personal commun.

stages F– through I (Keefe and Able, 1993), based on degree of eye migration.

Incidence of feeding and gut fullness were also examined, as a function of 2-h time blocks. Gut fullness (F) was recorded as 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full. Incidence of feeding was recorded as the percent frequency of larvae that had prey in their guts (i.e. $F > 0$), in relation to the total number of specimens examined in a time block.

A total of 550 oceanic larvae were examined. Of these, 18 were excluded from analysis because large portions of their guts were missing, and 11 were excluded because their primitive condition likely impaired their ability to ingest prey (Blaxter, 1986; Gadomski[2]). Primitive characteristics included presence of yolk sac, absence of eye pigment, and undeveloped mouth. Evidence of prey ingestion was lacking in the 29 excluded larvae. This study was based on 521 oceanic larvae that were deemed to be functionally intact.

A second series of collections were examined to determine the feeding ecology of summer flounder larvae as they enter an estuarine nursery habitat. Metamorphic larvae were collected from plankton entering the Great Bay–Little Egg Harbor (New Jersey) estuary (Fig. 2) during fall, winter, and spring from 1989 to 1995. Most estuarine specimens (71.4%) were collected between November and January. The remainder were collected between February and June, and in October. Stationary plankton nets (1-m diameter, 1.0-mm mesh) were set for 30 min, at the surface and just off the bottom, on nocturnal flood tides, from a bridge across Little Sheepshead Creek (Szedlmayer et al., 1992; Keefe and Able, 1993). This site is characterized by Atlantic Ocean water on flood tides (Charlesworth, 1968, cited in Szedlmayer et al., 1992); thus larvae were likely captured as they entered the estuary from the ocean, or soon after.

Estuarine specimens were preserved in 95% ethanol, and they remained in ethanol until their examination. Specimens were processed as above. Because all estuarine specimens were metamorphic (ME), morphological stages were recorded in terms of Keefe and Able's (1993) metamorphic stages: F– through I. The estuarine portion of this study was based on 119 specimens.

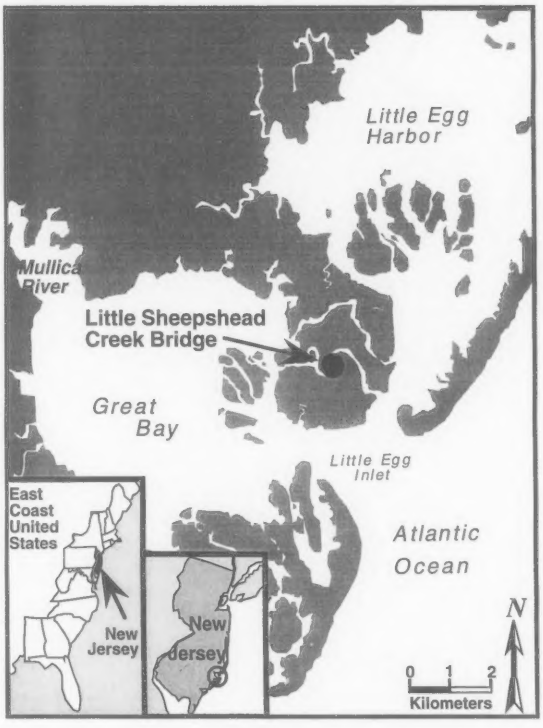

Figure 2

Location of the estuarine site in Little Sheepshead Creek, New Jersey, where metamorphic summer flounder, *P. dentatus*, were collected. (Figure by K. W. Able, Rutgers University.)

Results

Preflexion (PF) larvae were the dominant morphological stage in oceanic collections, accounting for 84.3% of the specimens (Table 1). Later morphological stages were progressively rarer, with flexion (FLX) larvae accounting for 12.5%, postflexion, premetamorphic (PM) larvae accounting for 1.7%, and metamorphic (M) larvae accounting for 1.5% of the oceanic specimens in this study. Although greater than 33% of the larvae in each morphological stage contained prey in their guts, stages PM and M were combined for dietary analyses because of their small representation in these collections and similarity in diet.

Larval lengths that were recorded at the time samples were sorted (usually within 12 months of collection) were compared with lengths at the time of examination in order to estimate shrinkage. Comparisons based on 329 specimens defined mean shrinkage as 13.7% (SD=5.83).

Diet of preflexion (PF) larvae

The dominant stage in this study, PF, was represented by a total of 439 specimens: 56.9% contained recognizable prey, and 43.1% had empty guts. Lengths at the time of examination ranged from 1.9 to 6.9 mm SL (Table 1).

[2] Gadomski, D. 1995. Columbia River Research Laboratory, National Biological Service, 5501A Cook-Underwood Road, Cook, WA 98605. Personal commun.

Table 1

Feeding incidence and number of prey ingested by summer flounder, *P. dentatus*, larvae by time block, habitat, and larval stage. OC = oceanic, ES = estuarine, PF = preflexion, FLX = flexion, PM = premetamorphic, and M = metamorphic (oceanic). Estuarine metamorphic stages are as defined by Keefe and Able (1993). Numeric data exclude copepod eggs that appeared to have been ingested incidentally by metamorphic larvae.

	Habitat type	No. larvae examined	Standard length (mm)			No. larvae with food	Percentage feeding	Total no. food items	No. food items per feeding larvae
			mean	SD	range				
Time block (h)									
0000–0159	OC	67	3.8	1.22	2.3–7.5	11	16.4	40	3.6
	ES	15	11.4	1.29	8.6–13.4	1	6.7	1	1.0
0200–0359	OC	18	4.5	1.04	3.4–6.7	2	11.1	3	1.5
	ES	11	12.3	1.91	8.8–14.6	1	9.1	1	1.0
0400–0559	OC	60	4.8	1.35	2.2–7.2	5	8.3	7	1.4
	ES	11	11.3	0.97	9.5–12.9	2	18.2	3	1.5
0600–0759	OC	44	4.3	1.39	2.6–7.6	24	54.5	104	4.3
	ES	2	10.3	0.44	10.0–10.6	0	0.0	0	0.0
0800–0959	OC	10	4.1	0.76	3.2–5.3	10	100.0	46	4.6
1000–1159	OC	33	3.8	0.96	2.7–5.8	27	81.8	107	4.0
1200–1359	OC	39	3.7	1.23	2.1–8.0	38	97.4	259	6.8
1400–1559	OC	41	3.6	1.16	2.1–8.3	36	87.8	256	7.1
1600–1759	OC	67	3.6	0.70	2.6–6.2	47	70.1	168	3.6
1800–1959	OC	32	3.8	1.12	1.9–7.9	27	84.4	106	3.9
	ES	36	12.4	1.62	8.8–14.5	5	13.9	13	2.6
2000–2159	OC	60	3.9	1.37	2.3–9.0	42	70.0	258	6.1
	ES	39	11.9	1.48	8.1–13.9	5	12.8	12	2.4
2200–2359	OC	50	4.1	1.25	2.1–8.3	11	22.0	31	2.8
	ES	5	11.3	1.76	8.8–13.5	1	20.0	2	2.0
Larval stage									
PF	OC	439	3.6	0.85	1.9–6.9	250	56.9	1276	5.1
FLX	OC	65	5.6	0.75	3.7–7.2	22	33.8	86	3.9
PM	OC	9	6.6	0.92	4.8–7.6	4	44.4	17	4.3
M	OC	8	7.7	0.97	5.8–9.0	3	37.5	6	2.0
G	ES	47	11.9	1.74	8.1–14.4	9	19.1	19	2.1
H–	ES	34	12.0	1.51	8.8–14.6	3	8.8	7	2.3
H	ES	35	11.8	1.35	8.8–14.5	1	2.9	2	2.0
H+	ES	1	12.6		12.6	1	100.0	1	1.0
I	ES	2	13.3	0.71	12.8–13.8	1	50.0	3	3.0

Immature copepodites composed the bulk of the diet (61.4% Vol, 37.3% IRI; Table 2) of PF larvae. Copepod nauplii, the second most important prey, composed 20.0% (N and IRI) of the diet. Tintinnids, despite being the most abundantly ingested prey (28.7% N), ranked third in importance at 19.3% (IRI). Bivalve larvae and copepod eggs were the only other prey that accounted for >1% of the diet, and together they composed 21.7% (IRI).

The size of ingested prey was directly related to larval size. Only PF larvae, the smallest larvae, abundantly ingested small prey, i.e. tintinnids, copepod nauplii, copepod eggs, and bivalve larvae. Diatoms and dinoflagellates were also occasionally ingested (4.4% FO), although both were of such minor importance in the total diet that they were pooled into the "other" prey category. The mean number of prey found in the guts of PF larvae was 5.1 (SD=4.47, range: 1–25). For PF larvae, the ingestion of copepod eggs and invertebrate eggs was clearly independent of the ingestion of berried females. Visual cues of prey may be important for feeding larvae because grains of sand that visually "mimicked" bivalve larvae, in size, shape, and color, were ingested along with bivalve larvae by 4.4% of PF larvae.

Diet of flexion (FLX) larvae

A total of 65 FLX specimens were represented in this study: 33.8% contained recognizable prey, and 66.2% had empty guts. Lengths at the time of examination ranged from 3.7 to 7.2 mm SL (Table 1).

Immature copepodites dominated the diet of FLX larvae, regardless of method of analysis (Table 3).

Table 2

Diet of pelagic preflexion (PF) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 250 larvae.

Prey	%N	%Vol	%FO	%IRI
Tintinnids	28.7	3.3	37.6	19.3
Copepod nauplii	20.0	10.2	41.2	20.0
Copepodites	16.0	61.4	30.0	37.3
Calanoids	0.6	4.9	2.0	0.2
Cyclopoids	0.6	2.0	2.4	0.1
Copepod eggs	16.0	1.2	34.8	9.6
Bivalve larvae	12.1	14.8	28.0	12.1
Invertebrate eggs	3.7	0.9	11.6	0.9
Other	2.3	1.3	9.2	0.5

Table 3

Diet of pelagic flexion (FLX) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 22 larvae.

Prey	%N	%Vol	%FO	%IRI
Polychaete larvae	1.2	0.5	4.5	0.1
Copepod nauplii	2.3	0.2	9.1	0.2
Copepodites	68.6	66.7	86.4	92.8
Calanoids	13.9	27.5	18.2	6.0
Cyclopoids	3.5	1.9	9.1	0.4
Copepod eggs	3.5	<0.1	9.1	0.3
Bivalve larvae	5.8	2.8	4.5	0.3
Invertebrate eggs	1.2	0.4	4.5	0.1

The well-digested condition of copepodites precluded specific identifications, but most appeared to be calanoids. The only other prey category to represent more than 10% of the diet by any analysis was adult calanoid copepods, which despite accounting for 27.5% of dietary volume, composed only 6.0% IRI.

Tintinnids were not observed in the FLX larval diet, and other small prey items (copepod nauplii, copepod eggs, bivalve larvae, and invertebrate eggs) contributed little to the diet. The mean number of prey ingested by FLX larvae was 3.9 (SD=2.33, range=1–9).

Diet of oceanic premetamorphic and metamorphic (PM+M) larvae

A total of 9 PM and 8 M specimens were represented in this study: 44.4% of PM larvae and 37.5% of M larvae contained recognizable prey, and 55.6% of PM larvae and 62.5% of M larvae had empty guts. Lengths at the time of examination ranged from 4.8 to 7.6 mm SL for PM larvae and 5.8 to 9.0 mm SL for M larvae (Table 1). Combining the two stages (PM+M): 41.2% contained prey, and 58.8% had empty guts.

As with earlier morphological stages, immature copepodites were the primary prey for PM and M larvae, accounting for 50.1% of the diet (IRI). However, adult calanoid copepods and appendicularians, the secondary and tertiary prey (in terms of IRI), together contributed more than twice as much as copepodites to dietary volume (Table 4). Although it was not always possible to identify copepods to species, the most frequently ingested calanoid copepod appeared to be *Centropages typicus*. *Temora longicornis* and *Pseudocalanus* spp. also contributed to the diet. Appendicularians were only observed in the diet of PM and M larvae.

Table 4

Diet of pelagic postflexion, premetamorphic (PM), and metamorphic (M) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 7 larvae. Data exclude copepod eggs that appeared to have been ingested incidentally.

Prey	%N	%Vol	%FO	%IRI
Copepod nauplii	8.7	0.5	28.6	1.7
Copepodites	60.9	27.1	42.9	50.1
Calanoids	13.0	34.6	42.9	27.2
Appendicularians	17.4	37.8	28.6	21.0

The mean number of prey ingested by PM and M larvae was 3.3 (SD=2.14, range=1–6). Copepod eggs that were abundant in the gut of a single M-stage larva were excluded because they were probably ingested incidentally.

Incidence of feeding

An examination of incidence of feeding (defined as the percentage frequency of larvae with prey in their guts) in relation to 2-h time blocks over the course of

24 h (Table 1) revealed that pelagic larvae began feeding near sunrise in oceanic habitats. The presence of prey in larval guts reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.5% at 0600–0759 hours, the time block of sunrise for all collections. The only time during which incidence of feeding was 100% was 0800–0959. Throughout hours of full daylight, incidence of feeding remained high, ≥70%. Late afternoon or early-evening feeding may have buoyed the feeding incidence at 2000–2159, but evidence of recent feeding decreased sharply from 2000–2159 to 2200–2359 hours. During late night hours, the percentage of larvae that had prey in their guts gradually decreased from 22.0% at 2200–2359 to 8.3% at 0400–0559.

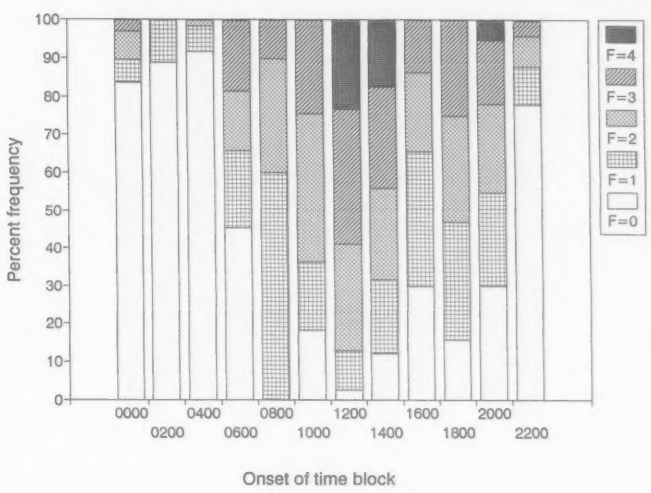

Figure 3

Gut fullness (F) of pelagic larval summer flounder *P. dentatus*, in the NW Atlantic Ocean, as a function of time of day (EST), where 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full.

Gut fullness

Because incidence of feeding data were generated from gut-fullness data (i.e. $F>0$), they provide a qualitative measure of gut fullness; however, gut-fullness data also provide direct estimates of the volume of prey in the gut over the course of 24 h (Fig. 3). Although larvae appeared to begin feeding at 0600–0759, full guts were not observed until 1200–1359. Maximum gut fullness ($F=4$) was only seen at 1200–1559 and 2000–2159. The only time block during which all larvae contained prey in their guts was 0800–0959.

Diet of metamorphic (ME) larvae in estuaries

The estuarine portion of this study was based on 119 metamorphic larvae (ME), representing metamorphic stages G through I (Keefe and Able, 1993) (with $n=47$ at stage G, $n=34$ at stage H–, $n=35$ at stage H, $n=1$ at stage H+, and $n=2$ at stage I, Table 1). The guts of 15 (12.6%) ME larvae contained recognizable prey, and 87.4% had empty guts. At the time of examination, larval lengths ranged from 8.1 to 14.6 mm SL.

Pelagic feeding was clearly demonstrated by > 85% of ME larvae. The primary prey of pelagic ME larvae was the calanoid copepod *Temora longicornis*, regardless of the method of analysis (Table 5).

The mean number of prey found in the guts of ME larvae was 2.1 (SD=0.99, range=1–4). The relatively good condition of some prey items in the guts of fish collected late at night suggests that some prey were likely ingested after dark.

Table 5

Diet of metamorphic (ME) summer flounder, *P. dentatus*, larvae collected from a New Jersey estuary, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 15 larvae. Prey were pelagic unless otherwise indicated.

Prey	%N	%Vol	%FO	%IRI
Polychaete larvae	3.1	0.7	6.7	0.4
Polychaete tentacles (benthic)	3.1	12.0	6.7	1.6
Cirripede larvae	3.1	0.2	6.7	0.3
Paracalanus parvus	3.1	2.0	6.7	0.5
Centropages typicus	6.3	13.6	6.7	2.1
Temora longicornis	46.8	55.3	53.3	86.2
Acartia sp.	3.1	2.9	6.7	0.6
Unidentified calanoids	6.3	3.7	13.3	2.1
Harpacticoids (benthic)	6.3	1.5	6.7	0.8
Mysids (diurnal migrants)	9.4	6.1	13.3	3.3
Oikopleura sp.	6.3	1.8	13.3	1.7
Unidentified prey remnants	3.1	0.2	6.7	0.4

Evidence of benthic feeding was observed only in late-stage metamorphic larvae (H+ and I). Of two late-stage larvae that had prey in their guts, one

single larva (stage I, 13.8 mm SL) clearly demonstrated benthic feeding, having ingested polychaete tentacles and harpacticoid copepods, and the other larva had ingested a mysid, a taxon noted for diurnal migrations (Newell and Newell, 1977). All late-stage larvae in estuarine collections displayed noticeably darker pigmentation than was observed in earlier stages.

Incidence of feeding in estuaries

A comparison of the incidence of feeding of oceanic and estuarine summer flounder larvae was limited to nocturnal collections and revealed strikingly different patterns (Table 1; Fig. 4). Between 1800 and 0759 hours the incidence of feeding of estuarine larvae never exceeded 20.0%, whereas values for oceanic larvae ranged from 8.3% to 84.4%. The greatest differences between oceanic and estuarine larvae were observed early in the night: at 1800–1959 and 2000–2159 the incidence of feeding in estuarine collections was significantly lower than in oceanic collections ($P<0.01$, $\chi^2=33.78$, 1 df, at 1800–1959; $P<0.01$, $\chi^2=30.99$, 1 df, at 2000–2159) (Fig. 4). Because most (63.0%) larvae in estuarine samples were collected between 1800 and 2159 (Table 1), these comparisons were not biased by low sample size.

Within estuarine habitats, incidence of feeding declined with metamorphic stage, from 19.1% at stage G to 2.9% at stage H (Table 1). Time was not a factor in this decline because the distribution of larvae of stages G, H–, and H was the same across early- (1800–2159), mid- (2200–0159), and late-night (0200–0559) collections ($P=0.18$, $\chi^2=6.22$, 4 df).

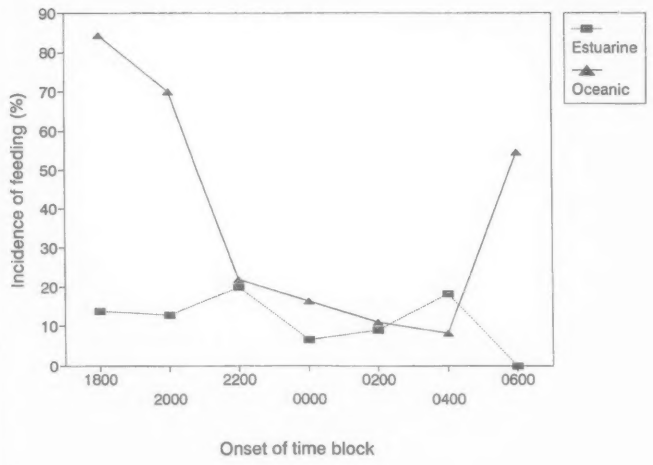

Figure 4

Incidence of feeding of larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and in a New Jersey estuary, as a function of time of day (EST) through the night. Data are based on a total of 331 oceanic and 119 estuarine specimens.

Discussion

The diet of all stages of oceanic summer flounder larvae was dominated by immature copepodites in the NW Atlantic Ocean. The size of other ingested prey was directly related to larval size. Small prey items such as copepod nauplii, tintinnids, and bivalve larvae, were important only in the diet of early (PF) stage larvae. Large prey items, such as adult calanoid copepods and appendicularians were important only in the diet of later (PM and M) stage larvae.

The diet of metamorphosing (ME) larvae that were collected in a New Jersey estuary was dominated by the calanoid copepod *Temora longicornis*.

These observations differ sharply from the diet of metamorphosing larval summer flounder in a North Carolina estuary (Burke, 1995). Burke (1995) reported that the larval diet was dominated by polychaetes and mysids. However, all larvae in the North Carolina study (Burke, 1995) were caught in estuarine nursery areas with benthic trawls, whereas in the present study oceanic larvae were caught with bongo nets, and estuarine larvae were caught with stationary plankton nets. Clearly these two studies captured metamorphosing larvae during different ecological phases of the transition from pelagic to benthic ecology. The diet of late-stage metamorphic larvae that demonstrated benthic feeding in an estuarine habitat in the present study was similar to the diet of comparable size larvae in Burke's (1995) study. The darker pigmentation of benthic-feeding, late-stage larvae suggests that this pigmentation may be a valid marker of adaptation to the benthic habitat in summer flounder, as has been observed in other species (Grover et al., in press).

The pelagic diet of a congener, the olive flounder,[3] *Paralichthys olivaceus*, may represent a more cogent comparison. In Wakasa Bay in the Japan Sea, Minami (1982) reported that

[3] The common and scientific names of fish species used in *Fishery Bulletin* are those recommended by the American Fisheries Society (Am. Fish. Soc. Spec. Publ. 20, 5th ed., 1991). The following names have been changed accordingly: Japanese flounder to olive flounder; *Parophrys vetulus* to *Pleuronectes vetulus*; *Isopsetta isolepis* to *Pleuronectes isolepis*; and *Limanda ferruginea* to *Pleuronectes ferrugineus*.

copepod nauplii were the most important prey in the diet of all premetamorphic stages of Japanese flounder larvae. However, Ikewaki and Tanaka (1993) later reported that olive flounder diet, in Wakasa Bay, was dominated by copepod nauplii only for first-feeding larvae and by appendicularians, *Oikopleura* spp., for later stages through early-metamorphic-phase larvae. Minami (1982) reported that appendicularians, copepods, and mysids were the dominant prey of early-, mid-, and late-metamorphic larvae, respectively. The sizable contribution of copepod nauplii to the diet of preflexion (PF) summer flounder larvae resembled the contribution observed in the diet of first-feeding (Ikewaki and Tanaka, 1993) and early stage olive flounder larvae (Minami, 1982). However, appendicularians, the dominant prey item for early-metamorphic larvae (Minami, 1982), and for all larval stages beyond first-feeding in olive flounder (Ikewaki and Tanaka, 1993), occurred only in the diet of premetamorphic and metamorphic (PM+M) summer flounder larvae.

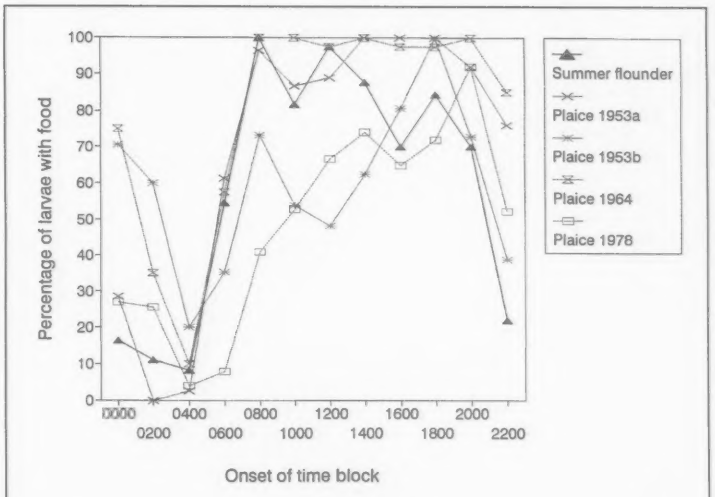

Figure 5

Incidence of feeding of pelagic larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and of pelagic larval plaice, *P. platessa*, in the Southern Bight of the North Sea and the English Channel, as a function of time of day. Sources of plaice data are as follows: 1953a = 48-h station, Shelbourne, 1953; 1953b = other stations (Shelbourne, 1953); 1964 = Ryland, 1964; 1978 = Last, 1978.

Pelagic summer flounder larvae that were collected in the NW Atlantic Ocean displayed a diurnal feeding pattern similar to that reported for several other flatfish larvae (e.g. plaice, *Pleuronectes platessa*: Shelbourne, 1953; Ryland, 1964; Last, 1978; dab, *Limanda limanda*: Last, 1978; English sole, *Pleuronectes vetulus*, and butter sole, *Pleuronectes isolepis*: Gadomski and Boehlert, 1984). Both incidence of feeding and gut-fullness data (Figs. 3 and 4) appear to confirm the visual nature of larval summer flounder feeding in oceanic collections. This is not surprising, because marine fish larvae are mostly visual feeders (Hunter, 1981; Blaxter, 1986; Huse, 1994). However, the optimal illumination level for feeding varies with species (Huse, 1994). For example, Atlantic cod, *Gadus morhua*, larvae feed preferentially at very low light levels, and turbot, *Scophthalmus maximus*, larvae feed preferentially at high levels of illumination, whereas plaice larvae feed over a wide range of illumination levels (Huse, 1994).

Within the flatfishes, additional relationships between illumination and larval feeding have been demonstrated. For example, sole, *Solea solea*, larvae can feed in the dark from the early posthatching stage (Blaxter, 1969). Oceanic collections of yellowtail flounder, *Pleuronectes ferrugineus*, larvae have shown that the highest incidence of feeding occurred between 1600 and 0100 (Smith et al., 1978). The near absence of feeding between 0700 and 1300 suggests that onset of feeding in yellowtail flounder larvae is triggered by something other than, or in addition to, illumination (Smith et al., 1978).

Data from oceanic collections in the present study suggest that the relationship between illumination and feeding of summer flounder larvae is much like that observed in one of the two flatfish species studied by Huse (1994). Laboratory observations are required to ascertain whether summer flounder larvae feed preferentially at high illumination levels or over a wide illumination range. However, an examination of incidence of feeding of pelagic plaice larvae (Shelbourne, 1953; Ryland, 1964; Last, 1978) in relation to comparable summer flounder data (Fig. 5) reveals similar patterns of feeding periodicity. From this, a similarity in optimal illumination levels for feeding for summer flounder and plaice larvae is suggested. To wit, pelagic summer flounder larvae would be expected to feed well over a wide range of illumination levels.

If the ecological analogy between plaice larvae and summer flounder larvae extends through metamorphosis, then a dramatic increase in light sensitivity (and a lower threshold light intensity for feeding) at metamorphosis (Blaxter, 1968) would be predicted for summer flounder. Limited field evidence supports this. A comparison of the incidence of feeding of oce-

anic and estuarine summer flounder larvae revealed strikingly different patterns (Fig. 4). Early in the night, incidence of feeding was much lower in estuarine collections. Fasting during metamorphosis, as has been noted in plaice (Riley, 1966; Lockwood 1984; Hamerlynck et al., 1989), may have contributed to this pattern. Plaice and sole have shown marked decreases in food-searching behaviors (distance covered per minute and time spent in feeding activity) at metamorphosis (Blaxter and Staines, 1971). Late at night, at 0400–0559, incidence of feeding in estuarine collections was double the rate seen in oceanic summer flounder collections (Fig. 4). A lower threshold light intensity for feeding at metamorphosis may have contributed to this, although small sample sizes of late-night estuarine collections preclude overreaching conclusions. Resolution of the threshold of light intensity for feeding of metamorphic summer flounder in a controlled laboratory setting could result in determination of optimal illumination levels at metamorphosis in aquaculture.

Metamorphosis has been considered a critical interval in the early life of some marine fishes (Thorisson, 1994). In the present study, the incidence of feeding of summer flounder larvae was observed to decline with metamorphic development to stage H. This suggests that the midpoint in the migration of the right eye (Keefe and Able, 1993) may be a critical period for summer flounder. In a laboratory study, a cessation of feeding was observed at stage G (Keefe and Able, 1993). However, cessation of feeding at metamorphosis may not place flatfish in any real danger of starvation (Lockwood, 1984). Metamorphic plaice larvae are capable of surviving without food for 7–25 d, without reaching the "point of no return" (Wyatt, 1972). Blaxter and Hempel (1963) have defined the "point of no return" as the point at which starved larvae become too weak to feed. Midmetamorphic summer flounder larvae are capable of surviving 56 d without reaching the "point of no return" (Keefe and Able, 1993). At metamorphosis and shortly thereafter flatfish may be more vulnerable to predation (van der Veer and Bergman, 1987; Witting and Able, 1993, 1995) than to starvation (Thorisson, 1994).

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Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia

Glenn A. Hyndes
Margaret E. Platell
Ian C. Potter
Biological Sciences, Murdoch University
Murdoch, Western Australia, 6150, Australia
E-mail address (for G. A. Hyndes): hyndes@central.murdoch.edu.au

Rodney C. J. Lenanton
Bernard Bowen Fisheries Research Institute
Western Australian Marine Research Laboratories
P.O. Box 20, North Beach
Western Australia, 6020, Australia

Abstract.—The age structure, growth and reproductive biology have been determined for the recreationally and commercially important King George whiting, *Sillaginodes punctata*, off southwestern Australia. The maximum lengths and ages, asymptotic lengths (L_∞), and growth coefficients (K) were 596 mm, 14 years, 532 mm, and 0.47, respectively, for females, and 555 mm, 13 years, 500 mm and 0.53, respectively, for males. Sexual maturity is attained by 50% of female *S. punctata* by ca. 410 mm in length, and by the majority of both female and male fish at the end of their fourth year of life. The monthly trends in the proportions of mature gonads and the prevalence of different oocyte stages and postovulatory follicles indicated that, in southwestern Australia, *S. punctata* spawns from June to September. Spawning is thus initiated when water temperatures are declining from their maxima. During the spawning period, many of the ovaries of large fish contained yolk vesicle and yolk granule oocytes, as well as hydrated oocytes or postovulatory follicles (or both), indicating that *S. punctata* is a multiple spawner. Furthermore, because hydrated oocytes or postovulatory follicles were often found together with large numbers of yolk granule oocytes, *S. punctata* presumably releases eggs in batches during the spawning period. Recruitment of *S. punctata* into sheltered nearshore waters (<1.5 m) commences in late September, three months after the onset of spawning, and continues until early November. When juvenile *S. punctata* reach ca. 1.5 years of age and ca. 250 mm, the legal minimum length for capture, they move out into slightly deeper waters (2–6 m) in marine embayments and estuaries. After attaining ages of ca. 4 years and lengths of ca. 370 mm, they then migrate from these waters, where fishing pressure is greatest, into regions near or around reefs at depths of 6–50 m, where spawning occurs. In contrast to *S. punctata*, the five other whiting species in southwestern Australian waters, which all belong to the genus *Sillago*, spawn between late spring and early autumn. In the case of the three *Sillago* species that undergo an offshore migration, this movement occurs at a relatively small size and young age and leads to their occupying open sandy areas. The implications of *S. punctata* habitat and biological data for fishery management are discussed.

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Fishery Bulletin 96:258–270 (1998).

The King George whiting, *Sillaginodes punctata*, which is the largest of the 31 species belonging to the Sillaginidae, occurs along the lower west and southern coasts of Australia (McKay, 1992), where it is a very important recreational and commercial species (see Kailola et al., 1993). Although a number of studies have been carried out on the biology of *S. punctata* (Scott, 1954; Thomson, 1957a; Gilmour, 1969; Robertson, 1977; Caton[1]; Cockrum and Jones[2]), these have concentrated mainly on fish caught in shallow waters, in which mature fish tend not to be found. Although Cockrum and Jones[2] obtained *S. punctata* from deeper waters, where spawning presumably occurs, data on the pattern of gonadal development, which is required to determine precisely the peak time and duration of spawning of this species, are very limited. Indeed, estimates of the timing and duration of spawning of *S. punctata* have been derived predominantly from backcalculations of daily growth increments of recently settled juveniles (Bruce, 1989; Bruce and Short, 1992; Jenkins and May, 1994; Fowler and Short, 1996). These latter studies, which were carried out off southeastern Australia, indicate that *S. punctata* spawns between early autumn and early winter. However, *S. punctata* is recruited into nearshore waters far earlier off South Australia than off southwestern Australia, which suggests that this species spawns later in the latter region (cf. Fowler and Short, 1996; Hyndes et al., 1996a).

Although age structures and growth parameters have been estimated for populations of *S. punctata* off southeastern Australia, the ages

[1] Caton, A. E. 1966. Preliminary synopsis of biological data on the Australian (spotted or King George) whiting (*Sillaginodes punctatus*) (Cuv. and Val.) 1829. CSIRO Technical Session, Department of Fisheries and Fauna Conservation Agenda Item 5, 43 p.

[2] Cockrum, K. S., and G. K. Jones. 1992. The reproductive biology and fecundity of King George whiting (*Sillaginodes punctata*) in South Australian waters, 1953–1988. South Australian Research and Development Institute Fisheries Research Paper 25, 18 p.

of fish in those studies were determined by the growth zones on scales or whole otoliths, which in neither case had been validated as being formed annually (Scott, 1954; Gilmour, 1969; Caton[1]; Jones et al.[3]). The present study demonstrates that, in the case of the populations of *S. punctata* in southwestern Australian waters, the growth zones on scales are difficult to discern and all of those on the otoliths of larger fish are only revealed after the otoliths have been sectioned. Data obtained from sectioned otoliths have thus been used to determine the age structure and growth rate of *S. punctata* on the lower west coast of Australia. Emphasis has then been placed on determining the length and age at first maturity, the location and period of spawning, and the period during which *S. punctata* is recruited into its nearshore nursery grounds. The implications of these biological data for managing this important species are then considered. Our results have been compared with those obtained for populations of *S. punctata* elsewhere in Australia. We have also compared aspects of the biology of *S. punctata* with those of the five other whiting species in the same region, all of which belong to the genus *Sillago* and, in the case of *S. schomburgkii* and *S. bassensis*, are fished both recreationally and commercially. This comparison enabled us to elucidate the extent to which age composition, growth, spawning period, and size-related shifts in habitat vary among the species comprising this abundant family.

Materials and methods

Small *S. punctata*, i.e. <300 mm, were collected from sites in nearshore marine waters (<1.5 m depth) between latitudes 32°00'S and 32°31'S on the lower west coast of Australia between June 1991 and May 1993 (see map in Hyndes et al., 1996a). Sampling was undertaken with a 21.5 m long seine net, which had a mesh size of 3 mm in the pocket. Large *S. punctata*, i.e. >300 mm, were obtained from recreational anglers, who were fishing between February 1993 and August 1996 in waters <50 m in depth between 31°55'S and 32°45'S. These anglers kindly supplied frozen carcasses, including gonads, after they had been filleted, together with a record of the date, location, and depth at which each fish had been captured.

The total length (TL) of each fish was measured to the nearest 1 mm. When a gonad could be identified as either an ovary or a testis, it was assigned to one of eight developmental stages, according to the criteria of Laevastu (1965): I = virgin; II = maturing virgin; III = developing; IV = maturing; V = mature; VI = spawning; VII = spent; and VIII = recovering or spent. However, multiple spawning by representatives of this species in each spawning season (see "Results" section) meant that it was often difficult to ascertain whether certain gonads should be recorded as stages V, VI, or VII. The data for these three stages, subsequently referred to collectively as mature gonads, were therefore pooled. It was not possible to recognize stage VIII gonads in males. Ovaries of the large female *S. punctata* collected in each month of the study were placed for 24 h in Bouin's fixative and then dehydrated in a series of ethanols. The midregion of each of these ovaries was embedded in paraffin wax, cut transversely (6 µm) and stained with Mallory's trichrome. The circumferences of 30 oocytes, where the section passed through the nucleus, were recorded to the nearest 5 µm by using the OPTIMAS (OPTIMAS Corp., 1994) computer imaging package. This enabled the diameters of these oocytes to be calculated. Because hydrated oocytes had collapsed as a result of freezing, their circumferences could not be measured. The oocyte measurements for fish in each calendar month during the three years of this study were pooled in order to provide histological data for up to 10 ovaries from each of those months. The terminology for the oocyte stages was adapted from that given in Khoo (1979).

The length at which 50% of female *S. punctata* first attained maturity (L_{50}) was calculated by fitting a logistic function to the proportion of mature fish in each 50-mm length interval in the spawning period of June to September (see "Results" section) by a nonlinear technique (Saila et al., 1988) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The logistic equation is

$$P_L = \left[1 + e^{(a+bL)}\right]^{-1}$$

where P_L = the proportion of fish with mature gonads at length interval L; and
a and b = constants.

The L_{50} was then derived from the equation

$$L_{50} = -ab^{-1}.$$

Preliminary examination of scales and sagittal otoliths collected from large *S. punctata* caught during the initial stages of the study showed that growth zones were often difficult to detect in scales, whereas at least some growth zones could be clearly discerned

[3] Jones, G. K., D. A. Hall, K. L. Hill, and A. J. Staniford. 1990. The South Australian marine scalefish fishery stock assessment; economics; management. South Australian Department of Fisheries Green Paper, January 1990, 186 p.

in whole otoliths. For this reason, sagittal otoliths were subsequently removed from each fish, cleaned, dried, stored, and used to estimate the ages of fish. In order to determine whether it was necessary to section otoliths to reveal all translucent zones, the number of translucent zones in the otoliths of 100 randomly selected *S. punctata*, in which whole otoliths displayed at least one such zone, were counted prior to and after sectioning. Of the otoliths that showed two to six translucent zones after sectioning, 19% exhibited one less zone prior to sectioning. Furthermore, in those otoliths that displayed seven or more translucent zones after sectioning, over 50% exhibited one less zone and 30% displayed between two and four fewer zones prior to sectioning. Thus, the otoliths of *S. punctata* had to be sectioned in order to discern all the translucent zones in those structures, a procedure that is also required for ageing several other fish species (e.g. Campana, 1984; Beamish and McFarlane, 1987; Casselman, 1987; Hyndes et al., 1992a). Otoliths were mounted and embedded in black epoxy resin and cut into approximately 0.8-mm transverse sections with a diamond saw. Sections were mounted on glass slides and their surface ground on sequentially finer grades of carborundum paper , with particle sizes ranging between ca. 30–10 μm. They were then coated with clear nail polish and examined microscopically under reflected light. The distance between the outer edge of the outermost translucent zone and the periphery of each otolith (marginal increment) was measured. This was expressed either as a proportion of the distance between the focus and the outer edge of the translucent zone, when only one translucent zone was present, or as a proportion of the distance between the outer edges of the two outermost translucent zones, when two or more translucent zones were present. Measurements were always made along the longest axis of each sectioned otolith and recorded to the nearest 0.05 mm. The number of translucent zones on each otolith was recorded. The birth date was designated as the midpoint of the main spawning period, based on the trends shown by gonadal and oocyte development (see "Results" section). Von Bertalanffy growth curves were fitted to the individual lengths of females and males at the estimated age at capture by a nonlinear technique (Gallucci and Quinn, 1979) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The von Bertalanffy equation is

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right],$$

where L_t = the length at age t (years);
L_∞ = the mean of the asymptote predicted by the equation;
K = the growth coefficient; and
t_0 = the hypothetical age at which fish would have zero length if growth followed that predicted by the equation.

The growth curves derived for females and males were compared by using a maximum-likelihood test (Kimura, 1980).

A fine mesh seine net, which was 5.5 m long and consisted of 1-mm mesh, was used in alternate weeks between late July and late December 1994 to collect recently settled *S. punctata* from sheltered nearshore sites in regions similar to those sampled by the 21.5-m seine net. The standard length (SL) of each of these fish on each sampling occasion was measured to the nearest 0.1 mm, except when the sample size was large, in which case measurements were made on a subsample of 100 fish.

Results

Age and growth

The mean marginal increment in sectioned otoliths with one translucent zone ranged from 0.42 to 0.54 between May and October, but then fell precipitously to 0.09 in November, before gradually increasing to 0.39 by April (Fig. 1). The marginal increments in otoliths with 2, 3, and 4–13 translucent zones also declined markedly between October and November and followed similar trends (Fig. 1). Thus, irrespective of the number of translucent zones in the otoliths, the marginal increment declined markedly and then rose progressively only once during a 12-month period, demonstrating that the translucent zones are formed annually.

In order to determine the size and age composition of *S. punctata* at different times of the year, the total lengths of fish caught in nearshore waters by seine net and in more offshore waters by anglers were pooled (Fig. 2A). Small *S. punctata* were first caught with seine nets in nearshore waters in early November, in which month their lengths ranged from 25 to 50 mm. By late December, the maximum length had increased to 68 mm (data not shown). The length range of the corresponding cohort, which comprised fish with otoliths that did not possess a translucent zone, increased to between 122 and 298 mm by August to October (Fig. 2A). Because the birth date of *S. punctata* was designated as 1 August (see below), the members of this cohort represent early 1+ fish. By November, a translucent zone had become discernible at the edge of the otoliths of these 1+ fish. The length range of this cohort ranged from 158 to

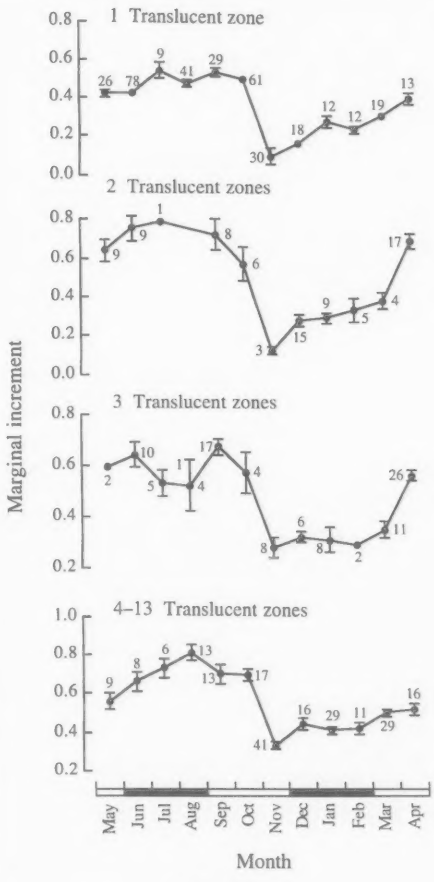

Figure 1

Mean monthly marginal increments ±1SE for sagittal otoliths of *Sillaginodes punctata*. Sample sizes are given for each month. In this Figure and Figure 5, the filled bars on the x-axis refer to winter and summer months, and the open bars to autumn and spring months.

282 mm from November to January, and from 251 to 403 mm from August to October, when this group of fish had just commenced their third year of life, and thus represents early 2+ fish (Fig. 2A). Between August and October, the lengths of 3+, 4+, and 5+ fish ranged from 340 to 425, from 403 to 480, and from 431 to 495 mm, respectively. *Sillaginodes punctata* attained maximum ages of 14+ and lengths of 596 mm in the case of females and maximum ages of 13+ and lengths of 555 mm with males.

Growth curves derived for female and male *S. punctata* (Fig. 3) differed significantly ($P<0.05$). The asymptotic length (L_∞) and growth coefficient (K) for females were 532 mm and 0.47, respectively, whereas for males they were 500 mm and 0.53, respectively (Table 1).

Table 1

Von Bertalanffy growth parameters (±95% CL) derived from length at age data for *Sillaginodes punctata* caught on the lower west coast of Australia. L_∞ is the asymptotic length, K is the growth coefficient, t_0 is the hypothetical age at which fish would have zero length, r^2 is the regression coefficient, n is the sample size.

	von Bertalanffy parameters				
	L_∞	K	t_0	r^2	n
Females	532.4 ±6.9	0.47 ±0.02	0.13 ±0.02	0.97	760
Males	500.1 ±7.7	0.53 ±0.02	0.16 ±0.02	0.96	637

Age and length at sexual maturity

For determining the length and age at maturity of female *S. punctata*, the data for mature (stages V–VII) and recovering or spent (stage VIII) ovaries were combined (Fig. 4). During the spawning period, which was determined as occurring from June to September (see below), the proportion of female fish with mature and recovering or spent ovaries increased sharply from 4% in the 350–399 mm length class to 71% in the 400–449 mm length class, and 100% in fish >500 mm (Fig. 4A). The length at which 50% of female *S. punctata* were mature, represented by the L_{50}, was 413 mm. Maturity was first attained by females at the end of their third year of life, when ca. 15% of fish possessed mature ovaries (Fig. 4B). However, by the end of the fourth year of life, the proportion of mature females had increased markedly to 72% and in subsequent years to 100%. A similar pattern was shown by the maturity stages for male fish (data not shown).

Gonadal and oocyte development

Because the vast majority of *S. punctata* did not reach maturity until the end of their fourth year of life, the following monthly trends shown by gonadal stages were derived from fish that were ≥3.4 years old and thus these fish were expected to reach maturity in the following spawning period. Between January and May, the ovaries of all female *S. punctata* ≥3.4 years old were at either stages III or IV (Fig. 5). Mature ovaries were found in over 70% of females by June and in 90 and 100% by July and August, respectively. The proportion of mature ovaries declined markedly to 43% in September, whereas the contribution of

recovering or spent ovaries (stage VIII) increased from 9 to 48% between August and September (Fig. 5). Female fish with mature ovaries were virtually absent by November, and those with stage-VIII ovaries represented only ca. 8% of the fish caught both in this month and in December. The gonadal development of males followed a similar trend to that of females (Fig. 5).

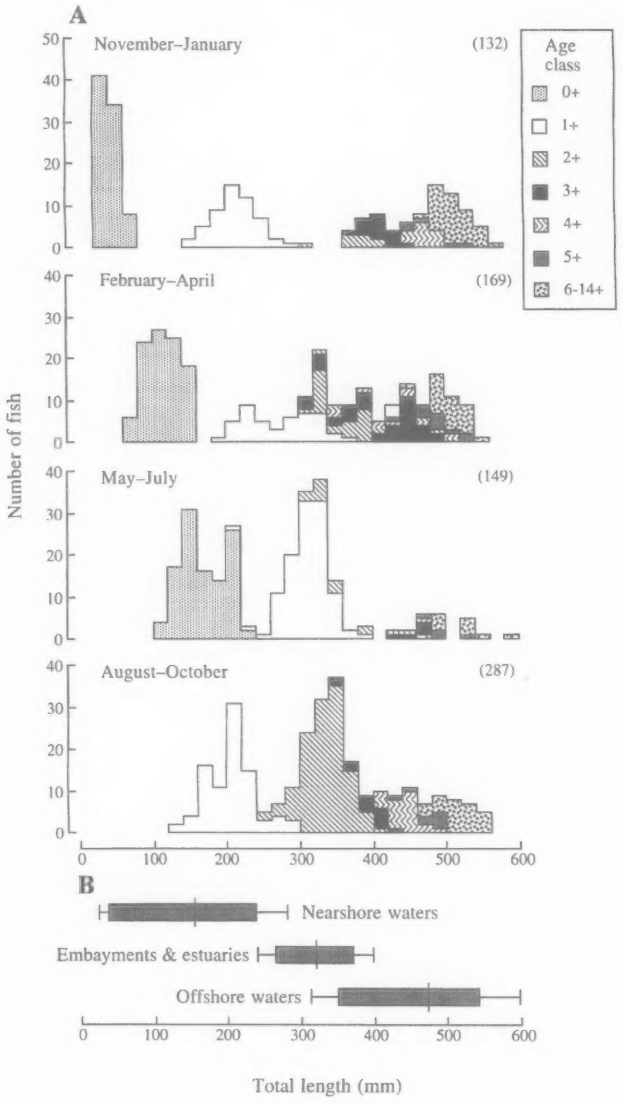

Figure 2

(**A**) Frequency histograms for total lengths of the different age classes of *Sillaginodes punctata,* from data obtained from samples collected by the 21.5-m seine net in nearshore marine waters and from anglers in deeper waters. Sample sizes are given in parentheses. (**B**) Median, 90 percentiles, and range of lengths for fish caught in shallow nearshore marine waters, deeper waters in marine embayments and estuaries, and in deeper and more offshore marine waters around reefs.

In each month, the oocyte diameters for *S. punctata* exhibited a well-defined mode between 50 and 80 µm (Fig. 6), which represents the perinuclear oocytes. Yolk vesicle and yolk granule oocytes first appeared in ovaries in April, when the diameters of these larger oocytes ranged between 255 and 430 µm. However, many other yolk vesicle and yolk granule oocytes were undergoing atresia. In the following month, the maximum oocyte diameter declined to 150 µm, reflecting the fact that no yolk vesicle or yolk granule oocytes were present. In June, the maximum diameter increased to 465 µm (Fig. 6), as a result of the development of yolk vesicle and yolk granule oocytes. These large oocytes were abundant between June and August, and many ovaries were dominated by yolk granule oocytes. The proportion of yolk vesicle and yolk granule oocytes declined in September, and the few remaining yolk vesicle and yolk granule oocytes that were present in October were at an advanced stage of atresia.

Hydrated oocytes that had collapsed during sectioning were found in large numbers in some ovaries between June and August. Because the ovaries in those months sometimes contained large numbers of postovulatory follicles, they had already discharged hydrated oocytes. Furthermore, hydrated oocytes and postovulatory follicles were occasionally found in the same ovary.

Juvenile recruitment and depth distribution

The new 0+ recruits of *S. punctata* were first caught in late September 1994. The minimum standard length of these fish remained at ca. 14 mm between 23 September and 3 November, before increasing to ca. 30 mm between mid-November and mid-December (Fig. 7). The maximum length of these new recruits increased progressively from 26 mm in late September to 64 mm by mid-December (Fig. 7).

Although the vast majority of *S. punctata* caught by anglers in embayments and estuaries at depths of 2–6 m were <370 mm in length and <4 years of age, those that were collected outside embayments and estuaries and in the vicinity of reefs at depths of 6–50 m were predominantly greater than this length and age (Fig. 8, A and B). Furthermore, *S. punctata* that contained mature (stages V–VII) or recovering or spent (stage VIII) gonads were caught predominantly in and around reefs and at the edges of seagrass beds adjacent to these areas, where water depths exceeded 6 m (Fig. 8).

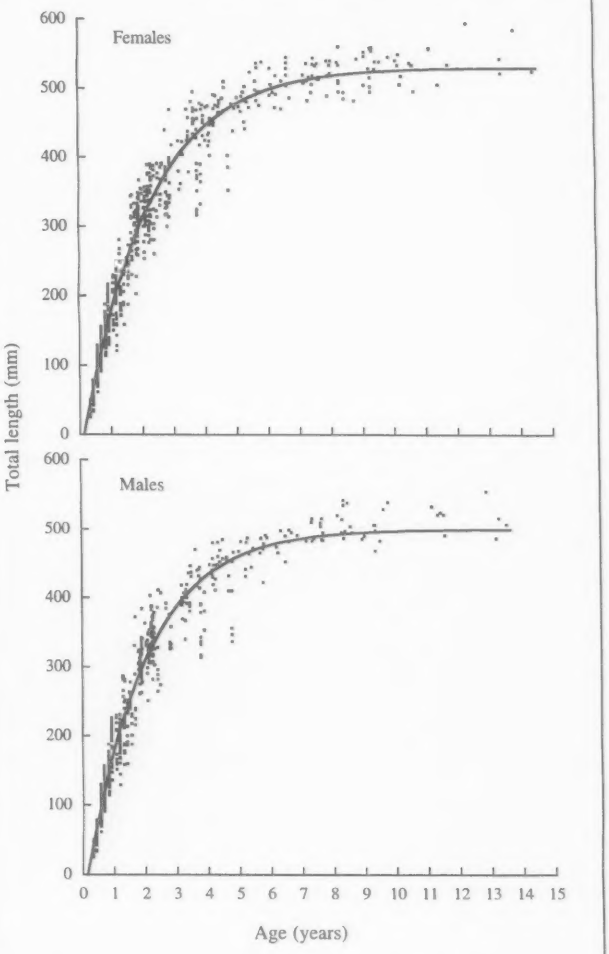

Figure 3

Von Bertalanffy growth curves fitted to total length-at-age data derived from sagittal otoliths of female and male *Sillaginodes punctata*.

Discussion

Sexual maturity and spawning period

Gonadal data indicate that, in southwestern Australia, female *S. punctata* reach maturity at the end of their fourth year of life or when they have attained a length of ca. 410 mm. This length far exceeds the 350 mm at which 50% of the members of this species reach maturity in southeastern Australian waters (see Cockrum and Jones[2]). However, the data of Cockrum and Jones[2] suggest that the length at maturity of *S. punctata* in southeastern Australia has declined since the 1950's as a result of fishing pressure, a trend that has been observed with increased fishing pressure in other species of teleosts (Wootton, 1990). Such a conclusion would be consistent with the fact that in southwestern Australia, where *S. punctata* is not at present as heavily exploited, the length at maturity (ca. 410 mm) is similar to that recorded in South Australia in the 1950's (Scott, 1954; Cockrum and Jones[2]).

Because large numbers of yolk granule and hydrated oocytes and postovulatory follicles were first found in the ovaries of large female *S. punctata* in June and were prevalent in ovaries through September, we conclude that this species spawns during this four-month period between early winter and early spring. Because the advanced oocytes present in ovaries in October and November were usually undergoing atresia, the spawning period of *S. punctata* rarely extends beyond September. The spawning of *S. punctata* during winter to early spring in southwestern Australia contrasts with the autumn and early winter spawning period found for *S. punctata* in southeastern Australia (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996; Cockrum and Jones[2]). Thus, although the duration of the spawning period of *S. punctata* is similar in both regions, it is initiated three months later on the lower west coast of Australia. It may thus be relevant that, in both regions, this species spawns when water temperatures are declining from their maxima and that this decline occurs more rapidly in southeastern Australia than on the lower west coast of Australia (Fig. 1 in Hyndes and Potter, 1996; Fowler[4]). The above

[4] Fowler, A. 1995. SARDI (South Australian Research and Development Institute), PO Box 120, Henley Beach, Adelaide, South Australia 5022, Australia.

spawning periods for *S. punctata* contrast with those of the majority of other temperate marine teleost species, including other whiting species, which typically breed at some period between late spring and early autumn (Morton, 1985; Vouglitois et al., 1987; Conover, 1992; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b). Because some of the estuaries of southwestern Australia often become closed from the sea by a sand bar in summer, a winter spawning period would allow the juveniles to become recruited into those estuaries (see "Nursery and spawning grounds" heading).

The presence in some ovaries of *S. punctata* of large numbers of yolk granule oocytes, together with either hydrated oocytes or postovulatory follicles, suggests that this species releases its eggs in batches. Furthermore, the presence of hydrated oocytes or postovulatory follicles, or both, in many of those ovaries which also contained advanced oocytes indicates that, although many oocytes were close to being released from those ovaries, others had recently been discharged. There is thus strong circumstantial evidence that *S. punctata* spawns on more than one occasion and possibly frequently during each breeding period. The conclusion that *S. punctata* is a multiple spawner (sensu de Vlaming, 1983) supports the conclusions of Cockrum and Jones[2] and parallels the situation recorded for several other sillaginid species (Morton, 1985; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b) and other teleosts in marine and estuarine waters in southwestern Australia (e.g. Hyndes et al., 1992b; Sarre et al., 1997).

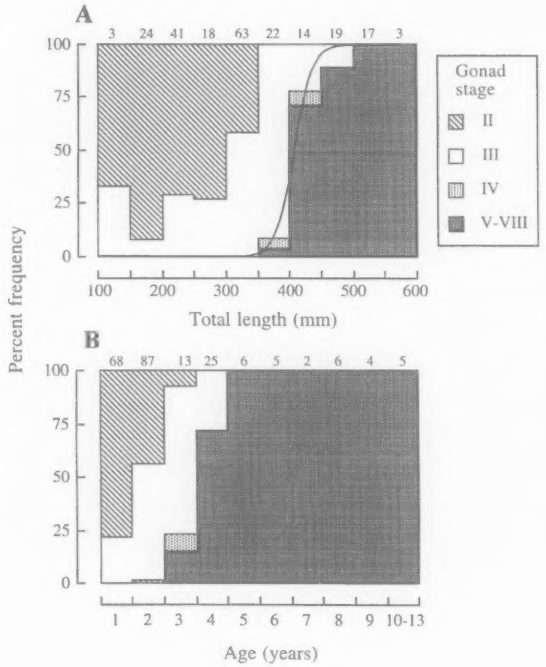

Figure 4

Percent frequency of occurrence of sequential stages in gonadal development in (**A**) each sequential 50-mm length class, and at (**B**) each age of female *Sillaginodes punctata* caught between June and September. The logistic curve, derived from the percentage of mature gonads for each length class, is also shown. Sample sizes are given above each length and age class.

Age and growth

The asymptotic lengths (L_∞) and growth coefficients (K) of female and male *S. punctata* in southwestern Australia, i.e. 532 and 0.47, and 500 mm and 0.53, respectively, lie within the range calculated for this species in southeastern Australia. However, these two parameters varied markedly in different localities within that latter region, i.e. 444 to 715 mm and 0.15 to 0.45 (Scott, 1954; Gilmour, 1969; Jones, 1980; Caton[1]; Jones et al.[3]). Such variation reflects either differences in the patterns of growth of this species in different locations or errors associated with deriving the age of fish from growth zones in scales or whole otoliths.

Sillaginodes punctata reaches a far greater size and age than the five other sillaginid species in southwestern Australia, all of which belong to the genus *Sillago* (Table 2). Furthermore, *S. punctata* does not attain maturity until it is four years old, which is far older than the age at which most of those *Sillago* species first spawn (Table 2). Because size and age at maturity are usually related to the length and age attained by teleosts (e.g. Beverton, 1992; Hyndes and Potter, 1997), this difference presumably reflects the greater size and age attained by *S. punctata*.

Nursery and spawning grounds

0+ *S. punctata* were first caught in the sheltered nearshore waters of marine embayments of southwestern Australia in late September, when their lengths ranged from 14 to 24 mm. Because this length range approximates that at which this species settles to a benthic habit (Jenkins and May, 1994; Bruce, 1995), these early juvenile fish would only recently have moved into those nearshore waters. The fact

Table 2

Asymptotic total length (mm), growth coefficient, maximum age (years), length at maturity (mm), age at maturity (years), and location of the nursery and spawning areas for *Sillaginodes punctata* and the *Sillago* species found in southwestern Australian waters. F = females; M = males.

	Asymptotic length (L_∞)		Growth coefficient (K)		Maximum age (T_{max})		Length at maturity (L_m)		Age at maturity (T_m)			
Species	F	M	F	M	F	M	F	M	F	M	Nursery grounds	Spawning grounds
Sillaginodes punctata	532	500	0.47	0.53	14	13	400	400	4	4	Sheltered nearshore	Reefs
Sillago bassensis	329	307	0.26	0.29	7	9	200	200	3	3	Exposed nearshore	Deep offshore
Sillago burrus	188	179	2.37	2.44	4	4	130	120	1	1	Sheltered nearshore	Shallow offshore
Sillago robusta	169	172	1.03	0.98	6	5	150	140	2	2	Offshore	Deep offshore
Sillago schomburgkii	333	325	0.52	0.53	7	7	200	180	2	2	Sheltered nearshore	Nearshore
Sillago vittata	331	312	0.43	0.45	7	6	140	130	1	1	Sheltered nearshore	Shallow offshore

that this size range of *S. punctata* was consistently observed in its specimens from nearshore waters between late September and early November (midspring), indicates that this species settles in its nearshore nursery grounds predominantly during this period. Thus, the first recruits of *S. punctata* enter those nearshore waters approximately three months after spawning is initiated, a time that corresponds to the time that the larvae of this species take to recruit into their nursery areas in South Australia (Bruce, 1989; Bruce and Short, 1992; Fowler and Short, 1996). Recruitment of juvenile *S. punctata* into the shallows commences far earlier in South Australian than in southwestern Australian waters, i.e. June vs. September, reflecting an earlier start to the spawning period, i.e. March vs. June (cf. Bruce, 1989; Fowler and Short, 1996). However, because the juveniles that are recruited into nursery habitats much farther east in Victoria are derived from a spawning that occurs in South Australia (Jenkins and Black, 1994; Jenkins and May, 1994), their larvae have to travel a far longer distance towards their nursery grounds than those recruited into nearshore waters of South Australia; thus recruitment commences far later in Victoria, i.e. September vs. June (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996).

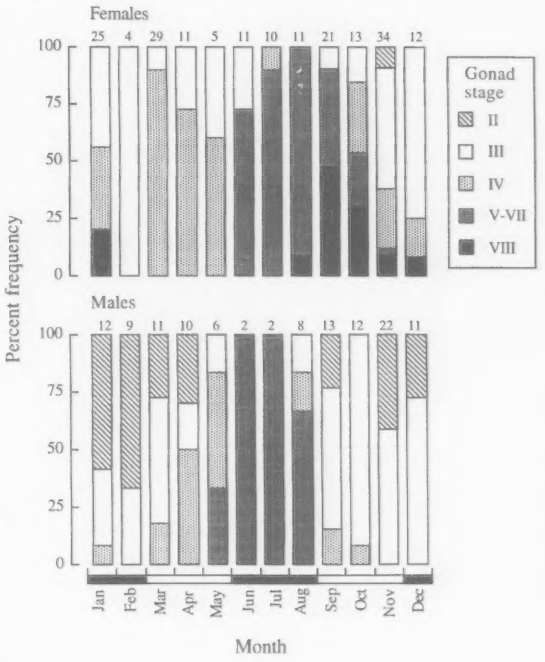

Figure 5

Monthly percent frequencies of occurrence of sequential gonadal development stages in female and male *Sillaginodes punctata* ≥3.4 years old. Numbers indicate sample sizes.

After settlement, large numbers of *S. punctata* remain in the sheltered nearshore marine waters of the lower west coast for about 1.5 years (Hyndes et al., 1996a). The fact that the densities of juveniles were far higher in these waters than in nearby exposed waters and even the shallows of estuaries (Hyndes et al., 1996a) indicates that the juveniles of this species prefer sheltered nearshore marine habitats. This conclusion is sup-

ported by the fact that juveniles of *S. punctata* are absent in nearshore waters along the southern coastline of southwestern Australia (Lenanton, 1982; Ayvazian and Hyndes, 1995), where the shoreline is more exposed to rough sea conditions (Hegge et al., 1996). The relative paucity of sheltered nearshore marine habitats on this coastline would account for the relatively high densities of juvenile *S. punctata* that are found in the relatively protected waters of estuaries in this region (Potter et al., 1993; Potter and Hyndes, 1994).

Estuaries along the southern coast of southwestern Australia, where the adjacent marine waters are exposed to wave and swell activity, may thus provide particularly important nursery habitats for *S. punctata*. Many estuaries in this region, however, become closed off from the sea during the summer and autumn, when, as a result of low freshwater discharge, a sand bar forms at their mouths (Lenanton and Hodgkin, 1985). It is thus relevant that *S. punctata* spawns during winter, because this would enable juveniles to enter those estuaries before their mouths become closed. This event parallels the situation with the mugilids *Mugil cephalus* and

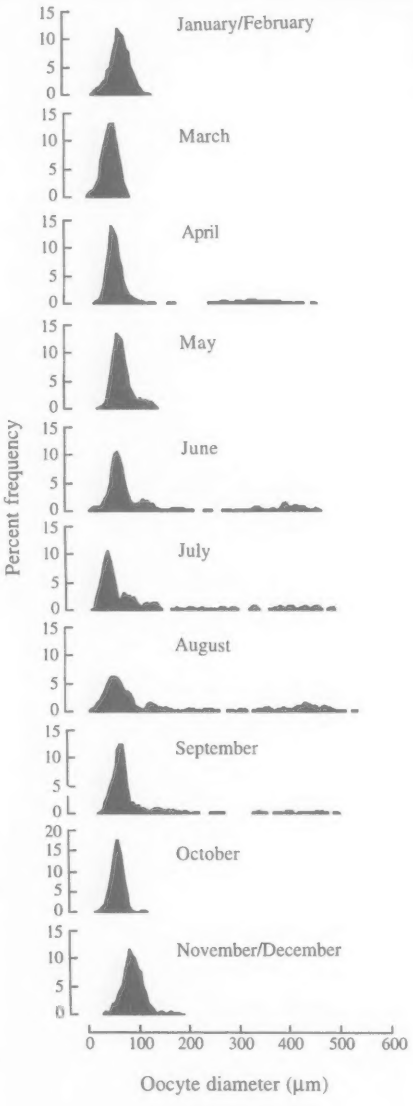

Figure 6

Monthly percent frequencies for oocyte diameters in ovaries of *Sillaginodes punctata*. Sample size in each month was 7–10 fish.

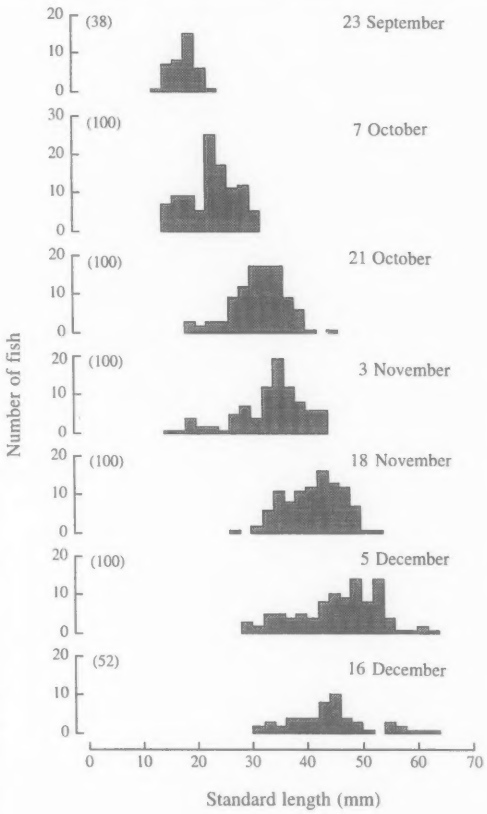

Figure 7

Frequency histograms for standard lengths of *Sillaginodes punctata* caught at two weekly intervals by the 5.5-m seine net in sheltered nearshore marine waters between September and December 1994. The numbers in parentheses represent the number of fish measured.

Aldrichetta forsteri, which also both spawn in winter in southwestern Australia and whose juveniles soon after enter estuaries in large numbers (Thomson, 1957b; Chubb et al., 1981).

Sillaginodes punctata typically remains in sheltered nearshore marine and estuarine waters until it reaches ca. 250 mm in length and ca. 1.5 years of age (Robertson, 1977; Potter et al., 1983; Loneragan et al., 1989; Potter et al., 1993; Potter and Hyndes, 1994; Hyndes et al., 1996a). Thus, unlike smaller species of whiting, such as *Sillago burrus* and *Sillago vittata*, which typically move offshore at lengths of ca. 100 mm and at ages of three to nine months (Hyndes et al., 1996a, 1996b), *S. punctata* remains in its nursery habitats for a far longer period. Because *S. burrus* and *S. vittata* reach maturity at the end of their first year of life, whereas most *S. punctata* first attain maturity at the end of their fourth year of life, this last species takes advantage of the productive waters of marine embayments or estuaries for a longer period before migrating out into spawning grounds in deeper marine waters.

Because the nursery areas of *S. punctata* are located initially in nearshore waters and subsequently in the deeper waters of marine embayments and estuaries, whereas adults occupy areas in and around reefs where water depths are generally greater, this species migrates offshore from shallow nursery grounds as it approaches the size and age at which it will become mature. A movement offshore as body size increases parallels that recorded for populations of *S. punctata* in southeastern Australia and for other whiting species (Scott, 1954; Gilmour, 1969; Robertson, 1977; Weng, 1986; Burchmore et al., 1988; Hyndes et al., 1996a; Caton[1]). Although anglers often caught *S. punctata* in deeper waters near reefs or at the edges of adjacent seagrass beds, they rarely caught them during extensive trawling over the expansive open, sandy areas of the same region where large numbers of other whiting species were caught (Hyndes et al., 1996a). The presence of mature and recovering or spent gonads in the larger members of *S. punctata* caught in areas around reefs also suggests that, unlike the three whiting species *Sillago burrus*, *S. vittata*, and *S. bassensis*, which migrate out into the more open and sandy areas of the inner shelf to spawn (Table 2; Hyndes et al., 1996b; Hyndes and Potter, 1996), *S. punctata* spawns in areas in and around reefs or at the edges of adjacent seagrass beds. Furthermore, whereas *S. burrus* and *S. vittata* move into spawning grounds ranging from 5–15 m in depth, and *S. bassensis* migrates into more offshore waters where the depth is 20–35 m deep (Hyndes et al., 1996a, 1996b; Hyndes and Potter, 1996), *S. punctata* spawns at depths that range from six to at least 50 m.

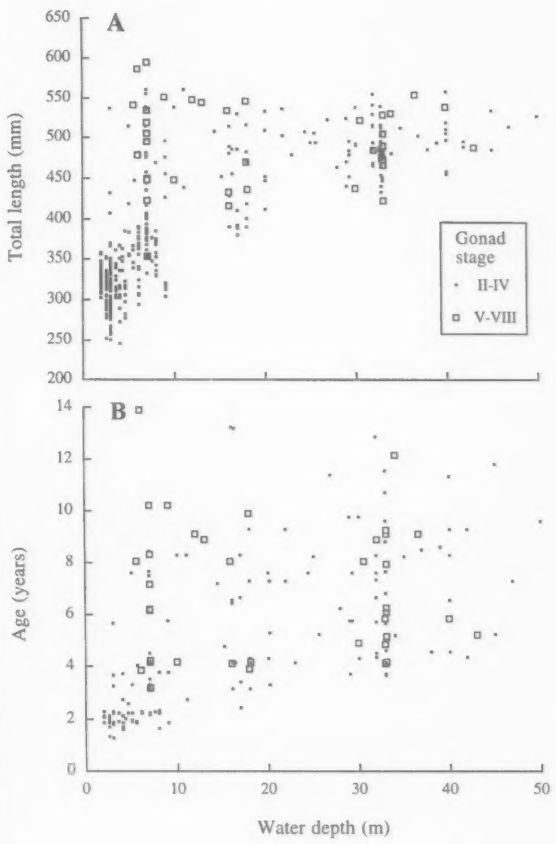

Figure 8

(**A**) Total lengths and (**B**) ages at capture, of female and male *Sillaginodes punctata* with immature (stages II–IV) and mature or recovering or spent (or both) (stages V–VIII) gonads collected at different depths by recreational fishers in the inner-shelf waters of the lower west coast of Australia.

Implications for management

Because *S. punctata* exhibits size-related offshore movements, that involve firstly a movement from nearshore nursery areas to deeper waters in marine embayments and estuaries and subsequently a move-

ment into areas around reefs farther offshore (Fig. 2B), this species essentially occupies three different habitats during the course of its life cycle. Any management plans for *S. puncata* must therefore take into account the need both to protect these habitats and to ensure that fishing pressure in those habitats where fishing occurs does not have a deleterious effect on the stock of this species.

The postlarvae of *S. punctata* settle predominantly in very sheltered nearshore waters of marine embayments and estuaries (Jenkins and May, 1994; Fowler and Short, 1996; Hyndes et al., 1996a; Hyndes, unpubl. data). However, *S. punctata* moves out into slightly deeper waters (2–10 m) in marine embayments and estuaries at ca. 1.5 years in age and at a total length of 250 mm (Fig. 2B). Because this latter length corresponds to the legal minimum length for capture (LML) of *S. punctata* on the lower west coast and approaches the LML of 280 mm on the south coast, this species does not become commercially and recreationally exploited until it has left its very shallow nursery areas and has entered deeper waters. This species remains in these slightly deeper waters until it reaches 350–400 mm (Fig. 2B) and is thus available for capture in marine embayments and estuaries when it is predominantly between 1.5 and 2.5 years in age. Because this species is most heavily exploited when it is in the deeper waters of marine embayments and estuaries, it is fished mainly during this relatively restricted period of its life cycle. From a management point of view, it is also relevant that the fishery in marine embayments and estuaries is based on fish that have not yet reached 410 mm, the length at which they typically first become mature. Subsequently, those *S. punctata* that have run the "gauntlet" of numerous fishermen in marine embayments and estuaries move farther out into areas in and around reefs in deeper waters where they attain maturity and where the reduced number of fishermen targeting this species makes it less susceptible to capture. Furthermore, the catches of *S. punctata* in the more offshore waters are further reduced in winter, when sea conditions are far less favorable for fishing and when, according to fishermen, *S. punctata* are less likely to take bait. Thus, because *S. punctata* spawns during winter, fishing pressure on this species is relatively low during the spawning period.

Because catch and effort statistics for the commercial fishery in southwestern Australia do not suggest that the catch rate for *S. punctata* is declining, this species would not appear currently to be overexploited in this region. However, the number of sheltered nearshore areas that act as nursery areas for *S. punctata* are limited and are often located in the type of region where marinas and other developments are likely to be proposed. Furthermore, recreational fishing effort is rising markedly, and the increasing use of larger vessels and more sophisticated equipment, such as global positioning systems (GPS), means that, particularly in deeper waters, fish are now beginning to be exploited to a greater extent. The resultant advances in fishing efficiency also mean that more sophisticated measures of effort are required to obtain reliable and comparable catch-per-unit-of-effort data for *S. punctata* from the recreational sector, which is ultimately expected to become the main exploiter of this resource.

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Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990–1995

Fred Julian
142 Sierra Way
Chula Vista, California 91911
E-mail address: fjulian@osiris.ucsd.edu

Marilyn Beeson
California Department of Fish and Game
330 Golden Shore, Suite 50
Long Beach, California 90802

Abstract.—Incidental kills of marine mammals, turtles, and seabirds are estimated for the California drift gillnet fishery for broadbill swordfish, *Xiphias gladius*, common thresher shark, *Alopias vulpinus*, and shortfin mako shark, *Isurus oxyrinchus*, and the set gillnet fishery for California halibut, *Paralichthys californicus*, and Pacific angel shark, *Squatina californica*, for the period July 1990 through December 1995. Estimates were based on observations made by National Marine Fisheries Service observers placed aboard commercial fishing vessels. Yearly observer coverage varied between 4% and 18% of estimated total effort. Total fishing effort-days per California Department of Fish and Game fishing block was used as the measure of effort for the drift and set gillnet fisheries. Incidental kill was estimated from observed data and estimates of total effort by using mean-per-unit and ratio estimators. Additional bycatch data collected by NMFS observers were used to derive kill estimates of marine turtles and seabirds.

In the drift gillnet fishery, seven out of 387 mammals observed entangled were released alive. In the set gillnet fishery, five out of 1,263 mammals observed entangled were released alive. Estimates of incidental kill are presented along with estimates of entanglement for species that were observed to be released alive. For the period under consideration, the estimated mortality for the drift gillnet fishery was over 450 marine mammals each year. A total of 20 turtles and 3 seabirds were observed entangled during the entire period. The most frequently entangled species in this fishery were common dolphins, *Delphinus* spp., and northern elephant seals, *Mirounga angustirostris*. Estimated cetacean mortality in the driftnet fishery decreased from 650 in 1991 to 417 in 1995; pinniped mortality decreased from 173 in 1991 to 116 in 1995. Estimated cetacean mortality in the set gillnet fishery ranged from a high of 38 in 1991 to a low 14 in 1993; pinniped mortality rose to a high of 4,777 in 1992 and then decreased to 1,016 in 1995. We postulate that there has been a decline in the number of pinnipeds and cetaceans in the setnet fishery owing to area closure. No similar proposal can be made for the driftnet fishery. The most frequently entangled mammals in the setnet fishery were California sea lions, *Zalophus californianus*, and harbor seals, *Phoca vitulina*. Six turtles and 1,018 seabirds were estimated entangled in this fishery during the NMFS Observer Program from July 1990 to December 1995.

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Two major gillnet fisheries in California are known to kill marine mammals, turtles, and seabirds incidentally: the drift gillnet fishery for broadbill swordfish, *Xiphias gladius*, common thresher shark, *Alopias vulpinus*, and shortfin mako shark, *Isurus oxyrinchus*, and the set gillnet fishery for California halibut, *Paralichthys californicus*, and Pacific angel shark, *Squatina californica*. Historically, concern was focused on incidental kill of seabirds, sea otters, *Enhydra lutris*, harbor porpoise, *Phocoena phocoena*, harbor seals, *Phoca vitulina*, and California sea lions, *Zalophus californianus*, in the setnet fishery (Salzman, 1989; Jefferson et al., 1994; Diamond and Hanan[1]; Hanan et al.[2,3]; Hanan and Diamond[4]). In recent years the driftnet fishery has received more attention because it interacts with more cetaceans (Barlow et al., 1994; Lennert et al., 1994). Estimation for the driftnet fishery has been possible because, in July 1990, the National Marine Fisheries Service (NMFS) implemented an observer program to monitor the marine mammal bycatch. Complementing the observer program was a project by the California Department of Fish and Game (CDFG) to develop estimates of total effort in the drift and set gillnet fisheries. Results from these programs were used to estimate incidental kill with stratified ratio and mean-per-unit estimation

[1] Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries, April 1. 1983 through March 31, 1984. NOAA/NMFS SWR Admin. Rep. SWR-86-15, 40 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[2] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California set net fisheries, April 1, 1984 through March 31, 1985. NOAA/NMFS SWR Admin. Rep. SWR-86-16, 38p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[3] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1988. Estimates of sea lion and harbor seal mortalities in California set net fisheries for 1983, 1984, and 1985. Final Rep. NA-86-ABH00018 submitted to NOAA Fisheries, SWR, 10 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[4] Hanan, D. A., and S. L. Diamond. 1989. Estimates of sea lion, harbor seal, and harbor porpoise mortalities in California set net fisheries for the 1986–87 fishing year. Final Rep. NA-86-ABH00018 submitted to NOAA Fisheries, SWR, 10 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

methods (Lennert et al., 1994; Perkins et al.[5]; Julian[6, 7, 8]). Separate estimates of entanglement are provided for species that had individuals released alive. This paper documents incidental marine mammal, turtle, and seabird kill estimates in these two California gillnet fisheries, based on data from the NMFS observer program and CDFG effort estimates for the period July 1990 through December 1994, and documents the process and methods leading to these estimates.

Methods

Data collection

National Marine Fisheries Service observer data, daily logbooks of commercial gillnet fishermen, and receipts of landed fish sales were used in marine mammal mortality estimation. NMFS observer data were collected by trained technicians aboard commercial gillnet fishing boats that had a Marine Mammal Protection Act (MMPA) Exemption Permit and that met minimum U.S. Coast Guard safety standards. There were two general observation categories: observation of randomly selected trips and observation of approximately every fifth vessel trip. In the setnet fishery, systematically selected trips were further divided. Notification prior to the setting of nets resulted in a preset, systematic observation rather than a postset, systematic observation where notification to the vessel was given after the nets were set (see "Discussion" section). NMFS observers recorded data on location, date, marine mammal entanglements, including location of mammals in the net (by thirds of the net—vertically and horizontally), gear, bycatch, and target species catch for each net pull observed during a trip (Lennert et al., 1994).

Observers recorded twelve net-related parameters for drift and set nets. They were net type (set, drift, float, or trammel), net material (monofilament, multifilament, or a combination), net strength (pounds test or twine size depending on strength code), strength code, net length (fathoms), net depth (number of meshes), stretched mesh size (inches), extender length (feet, float, and drift nets only), hanging line material (synthetic or natural fiber), percent slack in net, number of meshes hanging (between knots to the cork line), and hanging length (distance between knots on the cork line in inches). Not infrequently, a drift or set net will consist of panels of varying characteristics. In this case, observers would record characteristics on up to 5 different panels. Net characteristics for both fisheries are summarized in Table 1. Although the variability in these characteristics contributes somewhat to the variability in mortality estimates, the significant factors for mortality estimation are the amount of effort and the general location of the effort. For some species, e.g. pinnipeds, quarter of the year is also significant (Perkins et al.[5]).

Collected data were entered into a database file, checked for accuracy, and tabulated for mortality estimation (Tables 2–5). After an initial six month period, this observation method continued unchanged in both fisheries. Realized observation rates varied between 4.4% and 17.9% yearly, but observation rates were more variable if stratified by area and quarter. Observation in the driftnet fishery continued through December 1995, whereas observation in the setnet fishery terminated by July 1994 because of a significant decrease in fishing effort in that fishery (due to regulations that restricted areas open to gillnet fishing). Observer data were complemented by information from vessel logbooks and landing receipts (i.e. receipts from sales of landed fish).

Vessel logbooks were submitted monthly to CDFG and constituted the major source of information for estimation of total effort. Data for each logbook entry included date, vessel and permit identification, area fished by CDFG block number (Lennert et al. 1994), gear, number of sets made, and number and species of fish caught (CDFG blocks are typically 10' square; larger blocks are defined for areas further from shore). Logbook information was entered into a database by technicians and checked for accuracy by biologists. Fish species targeted for catch by the fishermen were determined and assigned to each data entry by CDFG personnel according to fish caught, gear used, and other pertinent factors. Purchases of landed fish by commercial fish buyers were recorded

[5] Perkins, P., J. Barlow, and M. Beeson. 1992. Pinniped and cetacean mortality in California gillnet fisheries: 1991. International Whaling Commission Scientific Committee working paper SC/44/SM14. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[6] Julian, F. 1993. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1992, rev. 2/94. International Whaling Commission Scientific Committee working paper SC/45/O22. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[7] Julian, F. 1994. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1993. International Whaling Commission Scientific Committee working paper SC/46/O11. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[8] Julian, F. 1995. Cetacean and pinniped mortality in California gillnet fisheries: preliminary estimates for 1994. International Whaling Commission Scientific Committee working paper SC/47/O5. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

Table 1

Observed net characteristics for the driftnet and setnet fisheries taken from nets characterized by one set of characteristics only (some nets may consist of two or more panels with differing characteristics). n = number of sets observed.

Characteristic	Driftnet fishery (n=2,932)	Setnet fishery (n=7,994)
Net type	All 2,932 were drift nets.	1,592 set nets and 6,278 1-panel trammel nets.
Net material	2,838 (97%) were multifilament nets.	7,520 (94%) were monofilament and 439 were multifilament.
Net strength and strength code	Twine size of 24 was used for 25% of the nets; size 27 was used for 36%, and size 30 was used for 22% of the nets.	3,203 (40%) nets with twine size 66, 10% with twine size 55, and 19.4% nets with unrecorded data.
Net length (m)	mean=1,784.9; SD=55.4; mode=1,828.8	mean=468.9, SD=164.7; mode=457.2
Net depth (meshes)	mean=128; SD=24; mode=130	mean=23.7; SD=8.9; mode=20 (n=7,880)
Mesh size (cm)	mean=52.1; SD=3.9; mode=53.34	mean=21.2 ; SD=2.2; mode=21.6 (n=7,968)
Extender length (m)	mean=11.48; SD=4.37; mode=11.30	Extenders not typically used; 98.4% of the nets did not use them.
Hanging line material	2,809 (95.8%) nets were of synthetic fiber.	7,628 (95.4%) nets were of synthetic fiber.
Percent slack	mean=45%; SD=5.4%; mode=50% (n=2,609).	No slack indicated for 38% of the nets. For nets with slack, mean=57%; SD=11%; mode=50% (n=4,986).
Meshes hanging	60% had 2 and 35% had 1 mesh hanging between knots tied to the cork line.	42% had 6, 26% had 4, and 17% had 6 meshes hanging between knots tied to the cork line.
Hanging length (cm)	mean=50.7; SD=14.6; mode=60.0 for distance between knots on the cork line.	mean = 38.4; SD=6.5; mode=38.1 for distance between knots on the cork line.

and those records were submitted to CDFG twice monthly. Landing receipts included information on species landed, weight by species, price, gear, area fished, and vessel and permit identification. Landing information was entered into a database and checked for accuracy. A target fish species was assigned to each entry. Logbook data, landing information, and NMFS observer data (date, set position, gear, and catch) were subsequently used in estimating effort.

Estimation of total effort

Fishing effort in both fisheries is an unknown quantity and absolute determination is impractical. Consequently, estimates of total fishing effort in each fishery were used to estimate incidental kill. These estimates were based on the combination of observer records, logbook data, and landing receipts. Effort was measured in "effort-days" which was defined as one day of fishing for one vessel. In the driftnet fishery, one effort-day was considered equivalent to setting and retrieving one net, generally 1828.8 m (1,000 fm) in length. (One vessel, targeting thresher shark, made two sets per day.) In the setnet fishery, typically two to four net settings, each of about 457.2 m (250 fm) in length, made up one effort-day. Days actually fished was used as the measure of total effort in each fishery because previous exploratory analysis determined that number of days of effort and general location of effort were significant factors in estimation of mortality (Perkins, et al.[5]). For some species, quarter of the year was also determined to be significant. These factors were available for all effort through the California Fish and Game Department and although other approaches to estimation (e.g. a modeling approach) can be developed, the current analysis is based on these factors. Data on other variables, such as total number of nets fished, total length of nets fished, or tons of target fish caught, were not readily available or contained additional variability due to nonsampling errors. Nonsampling

Table 2

Observed (obs) and (est) estimated cetacean, pinniped, turtle, and seabird mortality, stratified by year, in the California swordfish and shark drift gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of total mortality are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

Year	1990			1991			1992			1993			1994			1995		
Estimated days effort	4,078			4,778			4,379			5,442			4,248			3,673		
Observed days effort	178			470			596			728			759			572		
Percent observer coverage	4.4%			9.8%			13.6%			13.4%			17.9%			15.6%		
Observed trips effort	54			88			97			107			134			97		
	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV
Dall's porpoise	1	23	(0.95)	2	20	(0.67)	1	7	(0.92)	9	67	(0.44)	2	11	(0.64)	1	6	(0.92)
Pacific white-sided dolphin	3	69	(0.56)	5	51	(0.63)	3	22	(0.70)	2	15	(0.66)	3	17	(0.67)	1	6	(0.92)
Risso's dolphin	0	0	(—)	5	51	(0.50)	5	37	(0.48)	7	52	(0.51)	1	6	(0.91)	6	39	(0.57)
Bottlenose dolphin	0	0	(—)	0	0	(—)	3	22	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)
Striped dolphin	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.90)	0	0	(—)
Common dolphin (unknown stock)	4	92	(0.79)	7	71	(0.70)	5	37	(0.40)	4	30	(0.57)	1	6	(0.91)	0	0	(—)
Common dolphin (long beak)	0	0	(—)	0	0	(—)	2	15	(0.92)	0	0	(—)	1	6	(0.91)	6	39	(0.65)
Common dolphin (short beak)	4	92	(0.47)	37	376	(0.21)	39	287	(0.21)	24	179	(0.26)	25	140	(0.18)	36	231	(0.29)
Northern right whale dolphin	0	0	(—)	7	71	(0.41)	2	15	(0.65)	7	52	(0.39)	7	39	(0.42)	9	58	(0.59)
Killer whale	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.92)
Short-finned pilot whale	1	23	(0.95)	0	0	(—)	1	7	(0.92)	8	60	(0.54)	0	0	(—)	0	0	(—)
Baird's beaked whale	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.90)	0	0	(—)
Stejneger's beaked whale	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.91)	0	0	(—)
Hubbs' beaked whale	0	0	(—)	0	0	(—)	3	22	(0.53)	0	0	(—)	2	11	(0.64)	0	0	(—)
Mesoplodont beaked whale	1	23	(0.97)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)
Cuvier's beaked whale	0	0	(—)	0	0	(—)	6	44	(0.36)	3	22	(0.53)	6	34	(0.36)	5	32	(0.40)
Unidentified beaked whale	0	0	(—)	0	0	(—)	2	15	(0.65)	0	0	(—)	1	6	(0.90)	0	0	(—)
Sperm whale	0	0	(—)	0	0	(—)	1	7	(0.94)	2	15	(0.66)	0	0	(—)	0	0	(—)
Pygmy sperm whale	0	0	(—)	0	0	(—)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)
Unidentified *Kogia*	0	0	(—)	0	0	(—)	1	7	(0.92)	0	0	(—)	0	0	(—)	0	0	(—)
Minke whale	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.91)	0	0	(—)
Unidentified cetacean	0	0	(—)	1	10	(0.95)	1	7	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)
Unidentified dolphin	0	0	(—)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)
Unidentified whale	0	0	(—)	0	0	(—)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)
Steller sea lion	0	0	(—)	0	0	(—)	1	7	(0.92)	0	0	(—)	1	6	(0.91)	0	0	(—)
California sea lion	2	46	(0.99)	4	41	(0.58)	9	66	(0.34)	11	82	(0.42)	5	28	(0.40)	4	26	(0.45)
Unidentified sea lion	2	46	(0.97)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)
Harbor seal	1	23	(0.95)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)
Northern elephant seal	5	115	(0.44)	13	132	(0.25)	15	110	(0.24)	14	105	(0.26)	22	123	(0.23)	14	90	(0.25)
Loggerhead turtle	0	0	(—)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)
Leatherback turtle	1	23	(0.97)	0	0	(—)	2	15	(0.65)	2	15	(0.66)	0	0	(—)	4	26	(0.55)
Unidentified turtle	0	0	(—)	0	0	(—)	0	0	(—)	1	7	(0.93)	0	0	(—)	0	0	(—)
Seabirds (all unidentified)	1	23	(0.98)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.90)	0	0	(—)

errors, those not due to the sampling design, include, but are not limited to

1 Effort that is not recorded. This type of error may occur for several reasons, namely the times when no marketable target fish are caught during the entire day of effort and when a log entry is not made. The occurrence of this type of error implies that estimates of mortality are biased lower than actual mortality levels.

2 Incorrect reporting of effort location by fishermen. This type of error may bias estimated mortality either higher or lower.

Table 3

Observed (obs) and estimated (est) cetacean, pinniped, turtle, and seabird entanglement, stratified by year, in the California swordfish and shark drift gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of entanglement are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

Year	1990			1991			1992			1993			1994			1995		
	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV
Common dolphin (unknown stock)	4	92	(0.79)	7	71	(0.70)	6	44	(0.36)	4	30	(0.57)	1	6	(0.91)	0	0	(—)
Cuvier's beaked whale	0	0	(—)	0	0	(—)	6	44	(0.36)	3	22	(0.53)	6	34	(0.36)	6	39	(0.36)
Sperm whale	0	0	(—)	0	0	(—)	3	22	(0.94)	3	22	(0.69)	0	0	(—)	0	0	(—)
Humpback whale	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.91)	0	0	(—)
California sea lion	2	46	(0.99)	4	41	(0.58)	9	66	(0.34)	12	90	(0.39)	5	28	(0.40)	5	32	(0.40)
Unidentified sea lion	2	46	(0.97)	1	10	(0.95)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)
Loggerhead turtle	0	0	(—)	0	0	(—)	2	15	(0.66)	5	37	(0.49)	0	0	(—)	0	0	(—)
Leatherback turtle	1	23	(0.97)	1	10	(0.94)	4	29	(0.46)	3	22	(0.53)	1	6	(0.91)	5	32	(0.47)
Unidentified turtle	0	0	(—)	0	0	(—)	0	0	(—)	3	22	(0.93)	0	0	(—)	0	0	(—)
Seabirds (all unidentified)	1	23	(0.98)	0	0	(—)	1	7	(0.93)	0	0	(—)	1	6	(0.90)	0	0	(—)

3 Underestimation of effort from landing receipts. This type of error may occur when a landing receipt, in absence of additional information, is assumed to represent one effort-day (default-value).

A reliable determination of the magnitude of bias these errors cause in estimates of mortality rates has not been made; however, their characteristics indicate that estimates of mortality may be lower than actual values.

Once quarterly effort data were collected, computer programs developed by CDFG were used to assign target species to landing receipts on the basis of information provided by logbooks and observations (Beeson and Hanan[9]). Landing data were then confirmed or modified on the basis of logbook and observer data for the same target species, date, and vessel number. After all three data sources were compared, a day of effort was tallied for each record with a logbook entry or observer record. Landing receipts without corresponding logbook or observer entries three days before and after the receipt date were assumed to represent one day of effort. The numbers of days fished in each CDFG block were then tallied and the resultant data represented estimated total effort. Total effort was estimated quarterly and yearly. Delayed submission of data to CDFG was the primary reason that estimates of yearly effort differed from the sum of the quarterly estimates of effort.

[9] Beeson, M., and D. Hanan. 1996. Manuscript submitted to California Fish and Game. [Available from the authors at California Department of Fish and Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.]

Mortality estimation

Sampling design The NMFS observer program began in July 1990. Initially, the plan was to sample every fifth trip made by a drift gillnet vessel according to an assignment schedule. The order in which vessels with MMPA exemption certificates were scheduled to be observed was randomly selected. It became evident during the 1990 season that this scheme would not work because of logistical difficulties in adhering to the sampling plan.

Beginning in January 1991, gillnet vessel trips were selected according to the targeted coverage rate (20%), the availability of observer personnel, call-ins (fishermen called in prior to departure), and the ability to notify fishermen of their obligation to carry an observer. (Occasionally fishermen did not call the Observer Program administrator for possible observer assignment.) In addition, the NMFS Fisheries Observer Branch began monitoring vessel activity (arrivals and departures) to estimate observer coverage for placement purposes. If estimated observer coverage dropped below 20% for a vessel, the owner was notified of the obligation to carry an observer. In the setnet fishery, most fishermen were notified after their nets were set whether they would be required to carry an observer. As the program evolved, setnet fishermen began to expect an observer about every fifth trip.

Mortality estimation in the drift gillnet fishery In the swordfish and shark drift gillnet fishery, vessels made trips lasting from one to about 15 days so that

Table 4

Observed (obs) and estimated (est) cetacean, pinniped, turtle, and seabird mortality, stratified by year, in the California halibut and angel shark set gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of total mortality are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

Year	1990			1991			1992			1993			1994			1995[1]		
Estimated days effort	3,041			7,171			5,577			5,680			1,943			2,257		
Observed days effort	158			706			698			875			150			0		
Percent observer coverage	5.2%			9.8%			12.5%			15.4%			7.7%			0%		
Observed trips effort	406			2,233			2,123			2,642			547			0		
	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV	obs	est	CV
Harbor porpoise	4	37	(0.56)	5	38	(0.47)	6	48	(0.46)	2	13	(0.64)	1	14	(0.96)	—	14	(0.64)
Common dolphin (unknown stock)	0	0	(—)	0	0	(—)	2	15	(0.65)	0	0	(—)	0	0	(—)	—	—	(—)
Unidentified cetacean	0	0	(—)	0	0	(—)	1	8	(0.92)	0	0	(—)	0	0	(—)	—	—	(—)
California sea lion	67	867	(0.22)	142	1,842	(0.16)	338	3,418	(0.28)	237	1,942	(0.13)	109	905	(0.15)	—	724	(0.08)
Unidentified sea lion	1	23	(0.96)	6	109	(0.53)	7	54	(0.34)	0	0	(—)	0	0	(—)	—	—	(—)
Harbor seal	30	411	(0.23)	42	601	(0.23)	90	1,204	(0.47)	71	475	(0.13)	23	227	(0.33)	—	228	(0.13)
Northern elephant seal	13	119	(0.40)	3	30	(0.55)	7	51	(0.35)	11	70	(0.27)	2	16	(0.66)	—	47	(0.29)
Unidentified pinniped	2	42	(0.79)	3	30	(0.55)	7	50	(0.39)	7	32	(0.90)	1	8	(0.94)	—	17	(0.83)
Sea otter	3	27	(0.53)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	—	—	(—)
Green/black turtle	0	0	(—)	0	0	(—)	1	8	(0.92)	1	6	(0.90)	0	0	(—)	—	2	(0.61)
Loggerhead turtle	0	0	(—)	0	0	(—)	1	8	(0.92)	0	0	(—)	0	0	(—)	—	—	(—)
Leatherback turtle	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	1	8	(0.94)	—	—	(—)
Unidentified turtle	0	0	(—)	0	0	(—)	0	0	(—)	1	6	(0.90)	0	0	(—)	—	2	(0.61)
Pacific loon	0	0	(—)	1	13	(0.94)	0	0	(—)	0	0	(—)	0	0	(—)	—	—	(—)
Common loon	0	0	(—)	2	22	(0.68)	1	7	(0.92)	0	0	(—)	0	0	(—)	—	—	(—)
Unidentified loon	1	23	(0.96)	4	48	(0.48)	0	0	(—)	0	0	(—)	0	0	(—)	—	—	(—)
Western grebe	0	0	(—)	1	8	(0.92)	3	23	(0.70)	1	6	(0.90)	0	0	(—)	—	2	(0.61)
Unidentified grebe	0	0	(—)	0	0	(—)	4	31	(0.92)	1	6	(0.90)	0	0	(—)	—	3	(0.83)
Double-crested cormorant	2	18	(0.93)	0	0	(—)	1	7	(0.92)	0	0	(—)	1	8	(0.94)	—	—	(—)
Brandt's cormorant	2	41	(0.78)	36	409	(0.44)	14	279	(0.67)	3	13	(0.64)	2	16	(0.66)	—	3	(0.43)
Pelagic cormorant	1	33	(0.98)	1	8	(0.92)	0	0	(—)	0	0	(—)	0	0	(—)	—	—	(—)
Unidentified cormorant	9	132	(0.45)	15	450	(0.92)	9	68	(0.30)	5	32	(0.40)	0	0	(—)	—	10	(0.35)
Common murre	142	1,300	(0.21)	289	2,201	(0.27)	292	2,333	(0.28)	137	879	(0.32)	20	284	(0.29)	—	967	(0.32)
Unidentified alcid	1	9	(0.93)	0	0	(—)	0	0	(—)	0	0	(—)	0	0	(—)	—	—	(—)
Unid. seabird	0	0	(—)	2	22	(0.68)	3	23	(0.53)	1	6	(0.90)	0	0	(—)	—	3	(0.83)

[1] Estimates for 1995 were based on stratified rates from 1993 results.

when a trip was chosen to be observed, the NMFS technician observed all net pulls during the trip. A single net per day was set at dusk and retrieved before dawn. Net pulls and effort-days were equivalent units for this fishery. For estimation of incidental kill, the collection of observed trips during a year was treated as a random sample (an approximation) and a ratio estimator was used. Trips were treated as sampling units and the number of days per trip was treated as an auxiliary variable. Stratification by quarter of year or set location was not used for yearly estimates because previous exploratory analysis had not found this type of stratification to be significantly related to incidental kill. Yearly estimates, 1991–95, were calculated for each species observed entangled ("Results" section). Estimates for 1990 correspond only to the last two quarters of that year. Formulae from Cochran (1977) were used for estimating kill rate, $\hat{r}$, total incidental kill, $\hat{m}$, and variances:

$$\hat{r} = \frac{\Sigma_i k_i}{\Sigma_i d_i}, \quad (1)$$

$$\hat{\sigma}_r^2 = \left(1 - \frac{d}{D}\right)\left(\frac{1}{n}\right)\left(\frac{1}{d_{avg}^2}\right)\left(\hat{r}^2\sigma_d^2 + \hat{\sigma}_k^2 - 2\hat{r}\hat{\sigma}_{d,k}\right), \quad (2)$$

Table 5

Observed and estimated cetacean, pinniped, turtle, and seabird entanglement, stratified by year, in the California halibut and angel shark set gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of entanglement are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

Year	1990			1991			1992			1993			1994			1995[1]		
Unidentified sea lion	67	867	(0.22)	143	1,850	(0.16)	341	3,438	(0.28)	239	1,977	(0.13)	109	905	(0.15)	—	729	(0.08)
Harbor seal	30	411	(0.23)	43	615	(0.23)	90	1,204	(0.47)	71	475	(0.13)	23	227	(0.33)	—	228	(0.13)
Unidentified turtle	0	0	(—)	0	0	(—)	0	0	(—)	2	13	(0.64)	0	0	(—)	—	5	(0.59)
Common loon	0	0	(—)	4	48	(0.60)	1	7	(0.92)	0	0	(—)	0	0	(—)	—	—	(—)
Western grebe	0	0	(—)	2	22	(0.68)	3	23	(0.70)	1	6	(0.90)	0	0	(—)	—	2	(0.61)
Brandt's cormorant	2	41	(0.78)	41	494	(0.37)	20	321	(0.58)	5	25	(0.45)	2	16	(0.66)	—	9	(0.40)
Unidentified seabird	0	0	(—)	2	22	(0.68)	5	37	(0.41)	1	6	(0.90)	0	0	(—)	—	3	(0.83)

[1] Estimates for 1995 were based on stratified rates from 1993 results.

$$\hat{m} = D\hat{r}\,, \tag{3}$$

$$\hat{\sigma}_m^2 = D^2\hat{\sigma}_r^2\,. \tag{4}$$

Variables k_i and d_i represent the observed kill and number of days for the i^{th} trip; d_{avg} is the sampled mean number of days per trip; $\hat{\sigma}_d^2$, $\hat{\sigma}_k^2$, and $\hat{\sigma}_{d,k}$ are the sample variances and covariance of d_i and k_i; d and n are the observed number of days and trips, and D represents the total number of days of effort. The finite population correction factor, $(1 - n/N)$, where N is the total number of trips, was approximated by using $(1 - d/D)$ because the total number of driftnet trips was not determined during the estimation of effort.

Mortality estimation in the set gillnet fishery In the setnet fishery, a trip was selected and all net pulls during the trip were observed. Because greater than 99% of all observed set gillnet trips were one day in length, a trip was considered equivalent to an effort-day. Net pulls were not randomly sampled and total number of net pulls per trip was not recorded for unobserved trips, therefore a trip was considered the sampling unit. For observed trips, the overall average number of net pulls per trip (or effort-day) was 3.08 (CV=0.43), and the overall average number of marine mammal entanglements per trip was 0.48 (CV=3.10) during the NMFS Observer Program.

Researchers had previously shown (Perkins et al.[5]) that quarter of year and set location were significant predictors of sea lion and harbor seal entanglement. Consequently, estimation of incidental kill in the setnet fishery was stratified by area for all mammal species. The geographic area fished was divided into four strata: southern California, Channel Islands, Ventura, and central California. Central California included all effort south of Bodega Bay and north of Point Conception, 34°30'N (CDFG blocks 437–650). There was no legal coastal setnet fishing north of Bodega Bay. The Channel Islands stratum included all effort within CDFG blocks containing part of any Channel Islands (CDFG blocks 684–690, 707–713, 760–762, 765, 806–807, 813–814, 829, 849–850, and 867). The southern California stratum included all effort south of 33°50' N (blocks 718–918), excluding CDFG block 776 and the Channel Islands stratum. The Ventura stratum contained the remaining area. Incidental kill estimation for sea lions and harbor seals included additional stratification by quarter of the year for the southern California and Ventura areas because for these species, overstratification was not a problem.

Yearly estimates of incidental kill in the setnet fisheries were calculated for all species of marine mammals observed entangled (Tables 4 and 5). Estimates for turtles and seabirds were calculated by the same method. For each species, kill rate, r_s, and total incidental kill, m_s, were estimated for each area by using a mean-per-unit (MPU) estimator with effort-days as the sampling unit (Diamond and Hanan[1]). Formulae for MPU estimators and their estimated variances for each area are (Cochran, 1977)

$$\hat{r}_s = \frac{\Sigma_i k_{i,s}}{d_s}\,, \tag{5}$$

$$\hat{\sigma}_{r,s}^2 = \left(1 - \frac{d_s}{D_s}\right)\left(\frac{1}{d_s}\right)\hat{\sigma}_{k,s}^2\,, \tag{6}$$

$$\hat{m}_s = D_s\hat{r}_s\,, \tag{7}$$

$$\hat{\sigma}^2_{m,s} = D_s^2 \hat{\sigma}^2_{r,s}. \qquad (8)$$

The variable $k_{i,s}$ represents observed kill for the i^{th} observed day in stratum s, and $\hat{\sigma}^2_{k,s}$ is the sample variance of the observed kill. Variables d_s and D_s are observed and total number of days of effort in the stratum, respectively. Estimates of overall kill rate, $\hat{r}$, and total incidental kill, $\hat{m}$, across all strata, and variances, are then weighted averages:

$$\hat{r} = \frac{\Sigma_s D_s \hat{r}_s}{D}, \qquad (9)$$

$$\hat{\sigma}^2_r = \frac{\Sigma_s D_s^2 \hat{\sigma}^2_{r,s}}{D^2}, \qquad (10)$$

$$\hat{m} = \hat{D}r, \qquad (11)$$

$$\hat{\sigma}^2_m = D^2 \hat{\sigma}^2_r, \qquad (12)$$

where D is total number of days of effort during the year.

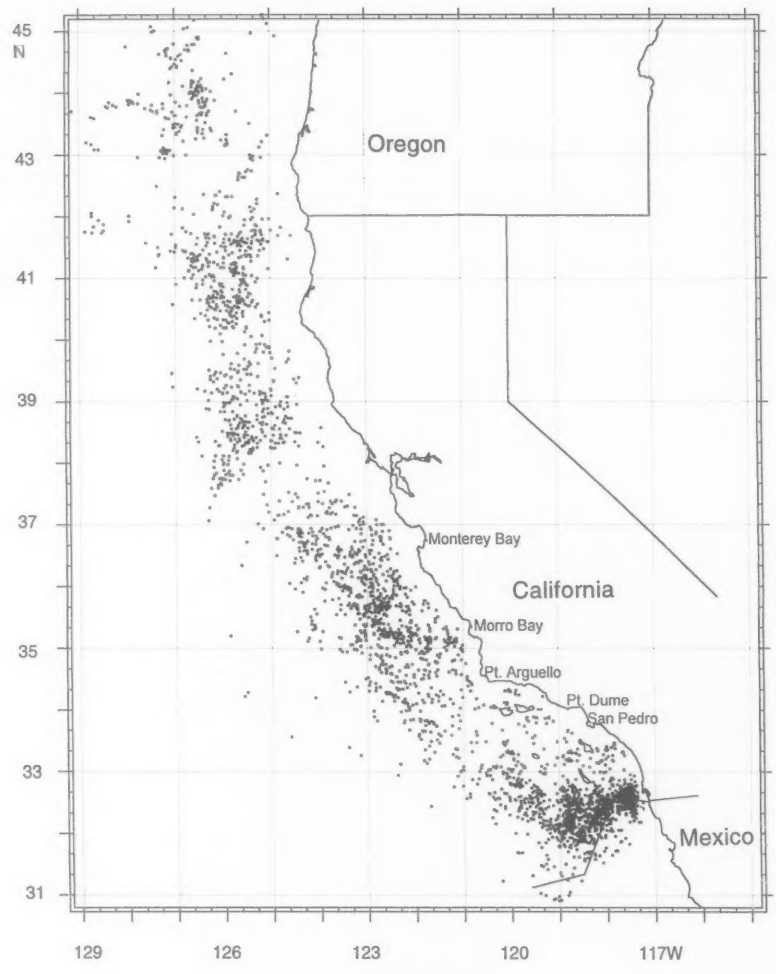

Figure 1

Approximate location of observed sets in the driftnet fishery during the period July 1990–December 1995.

Results

Driftnet fishery

During the observed period, the driftnet fishery was subject to area and time restrictions inside 370.4 km (200 nautical miles [n mi]) for effort that took place largely (80% of seasonal effort) from 15 August to 31 January. Between 1 February and 30 April, fishing effort was restricted to locations farther than 370.4 km offshore. From 1 May through 14 August (15 July for 1990–92) effort was required to be located farther than 138.9 km (75 n mi) offshore. For the remainder of the year, fishing was allowed within 138.9 km of shore. Since the beginning of the NMFS observer program in 1990, estimated total effort-days for the fourth quarter increased each year except for 1994. Combined effort for third and fourth quarters was consistently over 3,500 sets each year (Table 2). Even though there was effort along the entire California coast, the highest concentration of observed sets was south of 33°N (Fig. 1). Observer coverage in this fishery typically ranged between 10% and 15% of estimated total yearly effort for most areas and quarters. (Exceptions as low as 2% and as high as 25% were noted for some quarters and areas.) Bias of a ratio estimate is typically a problem in the case of small sample sizes such as may occur in a per-fishing block situation. Because sample size was generally quite large and stratification was not used, estimates were not corrected for bias. During the study period, July 1990–December 1995, nine (2%) of the 472 marine mammals observed entangled were released alive (one unidentified sea lion, one common dolphin, *Delphinus* spp., two California sea lions, one humpback whale, *Megaptera novaeangliae*, one Cuvier's beaked whale, *Ziphius cavirostris*, and

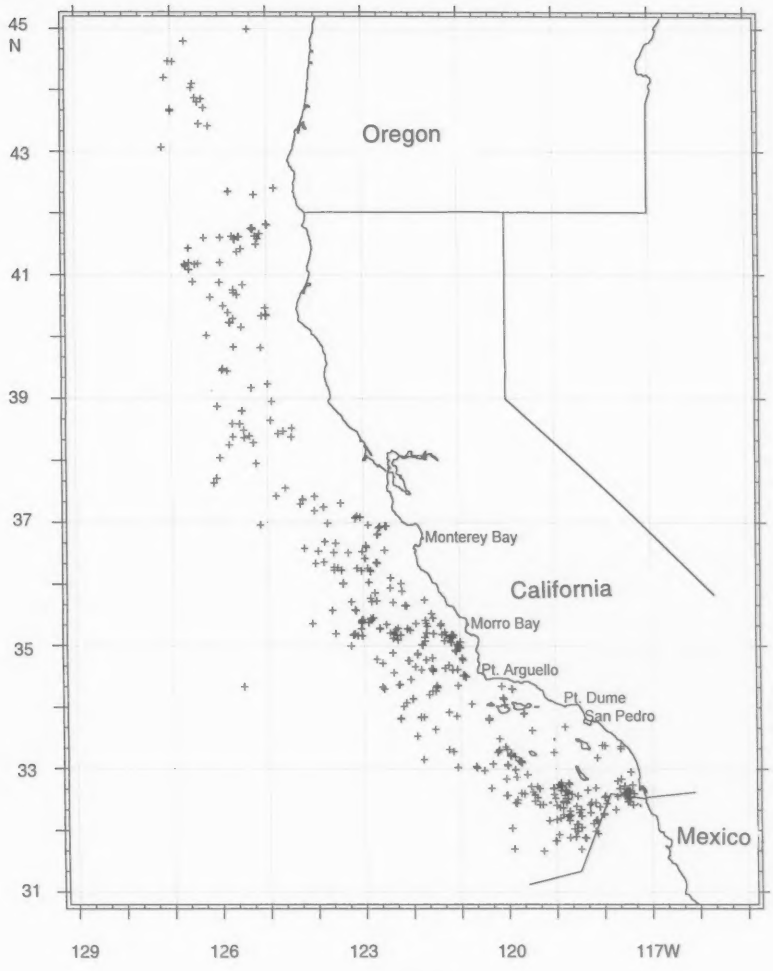

Figure 2

Approximate location of observed incidental marine mammal kills in the driftnet fishery during the period July 1990–December 1995, all species.

three sperm whales, *Physeter macrocephalus*). Observed mammal bycatch in this fishery consisted predominantly of common dolphins (196). Northern elephant seals, *Mirounga angustirostris,* were the second most commonly entangled mammal (83). The wide variety of mammal species incidentally entangled, over 25, is notable.

There was no statistically discernible trend in the estimates of total effort during the study period. Coefficients of variation for estimates of marine mammal incidental kill ranged from 0.18 to 0.95. The highest observed incidental kill in a single CDFG fishing block was in block 918, the southernmost block, which had 10% of the total observed mammal bycatch. Waters off central California west of 122°W longitude also had 10% of the observed mammal bycatch. Locations of marine mammal mortality from observer records indicate that mortality was concentrated in areas of heavy effort but geographically unrestricted (Figs. 1–2). On a quarterly basis, observed mammal bycatch and swordfish catch were correlated (r=0.8), but on a per set basis this correlation was not evident (r=0.0). This change in correlation is perhaps due to the inclusion of substantial effort (quarterly) versus per set consideration, i.e. both catch and bycatch are related to effort.

Observed seabird mortality was very low in the driftnet fishery (three kills observed during the period). Marine turtle entanglement was more common, with 25 observed (13 released alive). All but one of the 15 leatherback entanglements occurred north of 35°N latitude. Estimated turtle entanglement increased from 23 for 1990 to 81 for 1993 and then fell to 32 for 1995.

Setnet fishery

Mortality estimates in the setnet fishery pertain to fishing effort targeting halibut or angel shark. By law, effort targeting these species required gillnets with stretched mesh sizes of 21.6 cm (8.5 inches) or greater. This resulted in the elimination of 665 out of 8,614 observer records (net pulls) with mesh size less than 21.6 cm from the original data because they pertained to effort in another fishery. There were an additional 179 observed net pulls with no position data. This effort was assigned to geographic strata based on the specific vessel's known fishing grounds or was apportioned out to strata according to fishing effort from NMFS observer records with known positions.

From 1990 through 1993, estimated effort in the halibut and angel shark fishery was fairly stable with heavy setnet fishing effort along the southern California coast up to Pt. Conception (excluding the region from Rocky Pt. to Pt. Dume, where there was no commercial fishing, and an area around Newport

Beach; Fig. 3). There was also effort in the Morro Bay and Monterey Bay areas, as well as in some areas around the Channel Islands. Estimated effort for 1994 decreased sharply because gillnet fishing was banned inside the area within 5.6 km (3 n mi) of shore from Pt. Arguello south to the U.S.-Mexico border. During each year, observed mammal bycatch peaked during the second quarter, as did estimated total effort (Tables 4 and 5). California sea lions were the most frequently killed mammal (899), followed by harbor seals (257), northern elephant seals (36), and then harbor porpoises (18). Fourteen of the eighteen observed harbor porpoise mortalities occurred in the northern portion of Monterey Bay; three others were observed in the Monterey Bay area, and the remaining mortality was in the Morro Bay area (none was released alive). There were 1,025 seabird mortalities: 1 Pacific loon, *Gavia pacifica*, 5 common loon, *Gavia immer*, 5 unidentified loon, *Gavia* spp., 6 western grebe, *Aechmophorus occidentalis*, 5 unidentified grebe, *Podiceps* spp., 4 double-crested cormorant, *Phalacrocorax auritus*, 70 Brandt's cormorant, *Phalacrocorax penicillatu*, 2 pelagic cormorant, *Phalacrocorax pelagicus*, 38 unidentified cormorant, *Phalacrocorax* spp., 880 were common murre, *Uria aalge*, 1 unidentified alcid, *Alcidae*, and 8 unidentified seabirds, *Aves*. Of the common murre mortalities, 99% occurred north of Pt. Conception—predominantly in the Morro Bay area (Fig. 4). All other bird species were entangled south of Pt. Conception with few (12) exceptions (Tables 4 and 5). The six observed marine turtle kills were separated either in time or location, but four occurred offshore of Ventura. Locations of observer-recorded effort and bycatch indicated that no fished area was entirely free of mammal mortality due to gillnets (Figs. 3 and 5). Estimated total marine mammal mortalities for the setnet fishery rose from approximately 1,500 in 1990, to 4,800 in 1992, and fell to 1,300 in 1994.

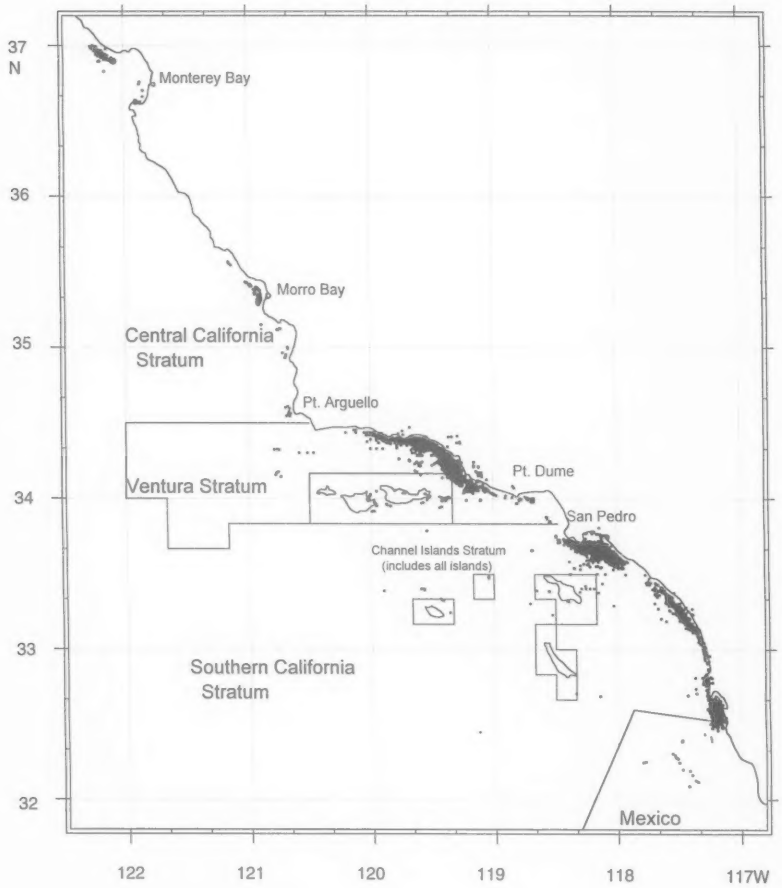

Figure 3

Approximate location of observed sets in the setnet fishery during the period July 1990–December 1995.

Discussion

Data collection and effort estimation

Although many resources were used to obtain accurate estimates of mortality and fishing effort, several significant difficulties were encountered in data collection and estimation of total effort. Difficulties in implementing the sampling plan included availability of observers and type of notification given to fishermen. Generally, observers were hired by the Program according to how much fishing effort was expected. Because this aspect of the program was well monitored, little seasonal bias was expected. Previous exploratory analysis has indicated that pre- and post-notification is a significant factor for the setnet fishery (Perkins et al.[5]). In this fishery, out of 2,588 days of observations,

only 74 (3%) were classified as preset notification. In the driftnet fishery, out of 3,338 observations, only 29 were categorized as postset notification. Because these data are so unbalanced in terms of type of notification, further analysis involving type of notification was not pursued. Apart from the overall difficulty of implementing an appropriate sampling plan, perhaps the most common difficulty was with accurate determination of location. Frequently, navigational equipment would not be "working" or was not available to the observer. In some cases, location was incorrectly relayed to the observer and under other circumstances observers were not able to determine location from major landmarks on shore owing to inclement weather. A second difficulty was that observers may not have been able to determine accurately the total number of animals or the species of the animals entangled in gillnets owing to obstruction of view by gear or crew. Also, mammals may have dropped out of a gill net prior to observation. Events of this type were considered nonsampling errors and may have biased estimates of incidental kill.

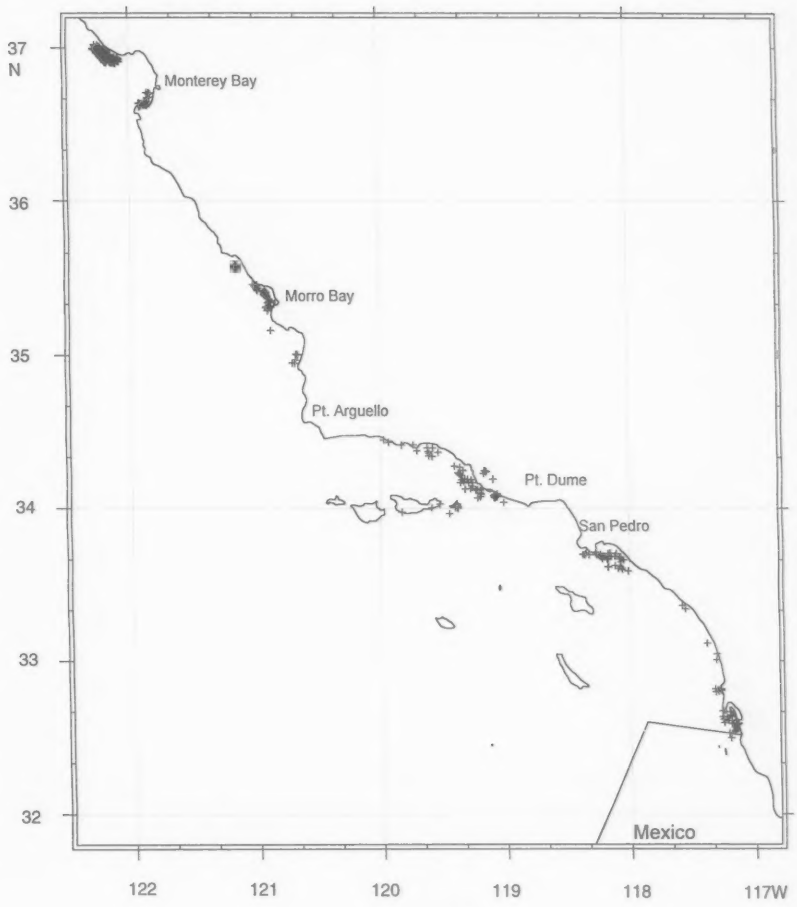

Figure 4

Approximate location of observed incidental seabird kills in the setnet fishery during the period July 1990–December 1995, all species.

Estimates of total effort were also subject to error, although they were treated as accurate for the purpose of bycatch estimation. They contained inaccuracies due to at least three nonsampling errors:

1 Completely unrecorded effort —A typical example of this was when no marketable target fish were caught during a trip and a logbook entry was not made. It was not possible to determine the size of this error; however, given that there were three chances for effort to be monitored (logbooks, observer records, and landing receipts), this error was probably small.

2 Absent or imprecise reporting of location—Even though location data were inaccurate, a record of effort was tallied. Thus, because estimates were not stratified by area in the driftnet fishery, this type of error had no impact on the determination of estimates of total effort or mortality for this fishery. (This type of error may be important in more detailed studies.) In the setnet fishery this type of error would not have produced an error in an estimate of total effort but may have produced errors in effort estimates for individual geographic strata. For purposes of mortality estimation, the setnet fishery was divided into four geographic strata, and effort without a recorded location was assigned, with good accuracy, to a stratum based on the vessel's known activity. If no information on a vessel's behavior was known, effort was divided among strata according to the proportion of effort in known locations. No additional error

was included in variance estimates because strata were large enough and vessels predictable enough that "assignment error" was most likely negligible compared with other assumptions. There was no way to determine accurately the direction of bias in effort estimates for each area.

3 Underestimation of effort from landing receipts—Underestimation of effort from landing receipts occurred when no effort was logged by fishermen or recorded by a NMFS observer for three days prior and subsequent to the date of the landing receipt. In these cases, a landing receipt was assumed to represent one day of fishing effort. Of the three types of nonsampling errors examined, this was potentially significant for the driftnet fishery because trips in this fishery may last over two weeks. For example, in 1993, the median length of a driftnet trip was 7 days; the mean was 6.8 (SE=3.3). Consequently, the number of times this approximation occurred was important. In the setnet fishery, with shorter trips, this assumption had less impact. It applied to multiple-day trips around the Channel Islands area, off the coast north of Santa Barbara, or when a fisherman held catch for more than one effort-day. Setnet trips were seldom more than a day in length because of catch storage and preservation limitations. In both the drift and setnet situations, the minimum effort representing a landing receipt was used, namely one effort-day, because a more appropriate approximation would have required a case-by-case investigation. The assumption contributed toward a possible negative bias of estimates of total effort and incidental kill.

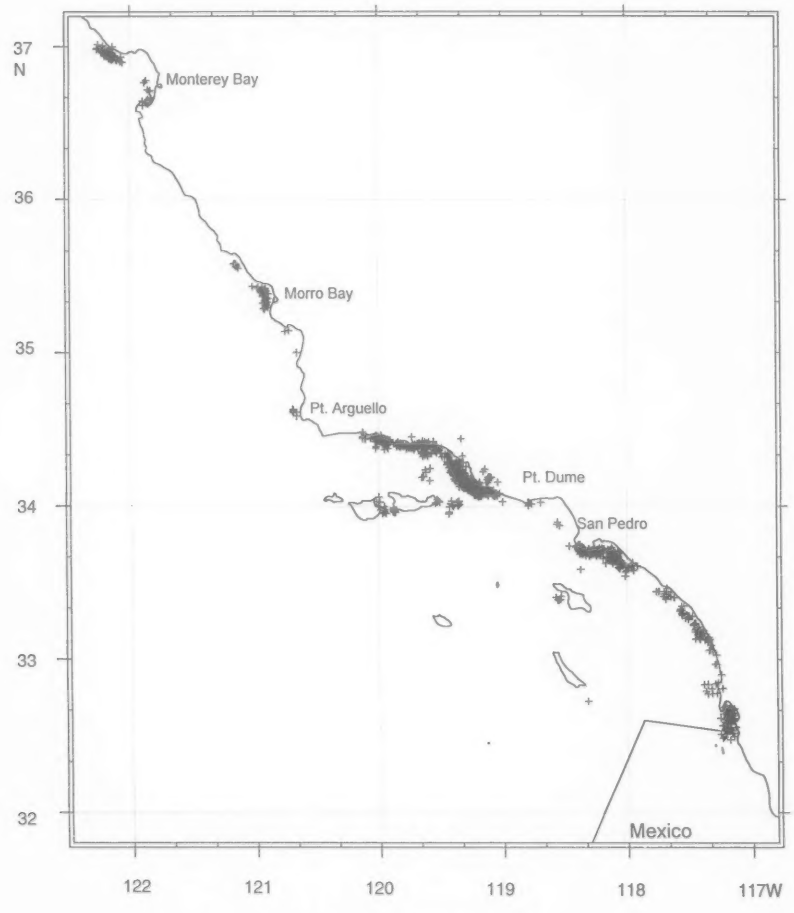

Figure 5

Approximate location of observed incidental marine mammal kills in the setnet fishery during the period July 1990–December 1995, all species.

Combined, these three difficulties in estimation of total effort may have produced a negative bias in estimates of total effort and, consequently, in estimates of incidental kill (i.e. current estimates of total effort may reasonably be considered a minimum). An accurate estimate of bias would be difficult and costly to obtain.

Mortality

Infrequent entanglement of marine mammals, turtles, and seabirds makes accurate estimation of species-specific incidental kill difficult. In spite of our good intentions, estimates may have been confounded by distribution of fishing effort or movement of species. In the future, the variability of estimates can be decreased by more strictly implementing a sampling plan. For some species, a posthoc analysis may be productive as information on movement and abundance of stocks becomes available. For infrequently entangled species, only increased observer coverage will improve estimation of incidental entanglement and kill rates.

In the driftnet fishery, the wide variety of cetacean species killed is attributable to the large geographic range of the mammals, nonselectivity of gear, and the amount and location of fishing effort. Cetacean bycatch in the driftnet fishery is greater and more diverse than for the setnet fishery because area of driftnet effort contains more diverse habitat than the area of setnet fishery. Data from recent years show that effort is increasing off the coasts of northern California and Oregon, and beginning in 1995, the state of Oregon allowed 10 driftnet fishing vessels to land fish in a limited number of Oregon ports (landings were not permitted prior to 1995). Yearly effort is expected to continue at 3,500–4,500 sets per year. The mortality rate averaged 0.11 (SD=0.25) mammals/set (or day) during the observer program, from January 1991 through December 1995; initial effort in 1990 was omitted because of low coverage rate. Incidental seabird catch has been almost nonexistent and there is currently no reason to expect an increase. The amount of seabird bycatch contrasts with the Japanese driftnet fishery in which many seabirds are incidentally caught (Ito et al., 1993), in part, because swordfish drift nets are extended below the surface, typically 11 m. The Japanese salmon drift nets, set at the surface, would naturally entangle more seabirds. Migration of seabirds in relation with the fishing season and effort location may play a role in seabird bycatch. No trend is evident in the estimated yearly turtle entanglements. Regarding cetaceans, at this time there are 10 species that are being entangled at a rate greater than potential biological removal (PBR) according to the U.S. Pacific Marine Mammal Stock Assessment Report (Barlow et al., 1995). The impact of driftnet mortality on individual cetacean stocks is examined in this report. In order to reduce entanglement of cetaceans, NMFS, in conjunction with driftnet fishermen and the California Department of Fish and Game, have implemented a Pacific Cetacean Take Reduction Team whose goal is to decrease cetacean bycatch.

Over the past five years, estimated effort in the halibut and angel shark setnet fishery was fairly stable until 1994, when a restrictive California voter proposition banned gillnet fishing within three miles of the coast from Pt. Arguello south to the US-Mexico border. Before 1994, effort in this fishery varied substantially during the year. Since early 1994, gillnet fishing has occurred mainly off Ventura, Morro Bay, and Bodega Bay (Fig. 3). There has also been some effort off Imperial Beach, near the US-Mexico border. Effort north of Pt. Arguello has not been affected by the 1994 resolution and is not expected to change.

Pinniped mortality in the setnet fishery was substantial during 1990–95. More pinnipeds were observed entangled in the setnet fishery than the driftnet fishery because effort coincided substantially with pinniped habitat. In particular, setnet effort around the Channel Islands and near the ports San Pedro, Ventura, and Santa Barbara frequently entangled pinnipeds. Effort in the driftnet fishery results in less overall pinniped entanglement by virtue of this effort being placed farther from shore. It is interesting to note, however, that entanglement of northern elephant seals in the driftnet fishery is substantially greater than for the setnet fishery because these mammals typically range greater distances from shore than do sea lions and harbor seals. Estimates of California sea lion and harbor seal mortality are expected to decline and then stabilize because of reduced effort south of Pt. Arguello.

Similarly, we expect the number of seabirds killed south of Pt. Conception to decline, because setnet effort was been pushed offshore 5.6 km (3 n mi) by regulation. There has been more bycatch of birds in the set fishery because the entangled species are typically resident and their habitat overlaps substantially with setnet effort. Driftnet effort results in few seabird entanglements because drift nets are retrieved after an overnight soak (set nets typically soak 24 hours) and drift nets are typically extended over 11 m below the surface. In addition, mesh size for drift nets is almost three times greater than mesh size for set nets, resulting in fewer entanglements. The mortality of common murres entangled in set nets is expected to continue at the same level. Murre were primarily observed entangled in the Monterey Bay area. The nets in this area are set on the bottom in typically 55.8 m (30.5 fm, SE=0.2 fm) of water. Using a chi-square (χ^2) test, we determined that there is some dependency between entanglement and soak time of the net ($P<0.05$). Odds of entanglement more than doubled for an increase from 1 to 2 days of soak time (reasonable checking for confounding factors was done). Turtles will continue to be entangled in the setnet fishery, but the number and rate of entanglement will be unknown because observer coverage in this fishery has been eliminated.

Acknowledgments

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ful and constructive comments were kindly provided by the reviewers. Finally, the cooperation of California gillnet fishermen, who allowed observers access to their boats, is sincerely appreciated.

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Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia

Joyce H. Landingham
Molly V. Sturdevant
Auke Bay Laboratory, Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
11305 Glacier Highway, Juneau, Alaska 99801-8626
E-mail address (for Molly Sturdevant, contact author): molly.sturdevant@noaa.gov

Richard D. Brodeur
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115-0070

Abstract.—First ocean-year feeding habits were determined for juvenile salmon (*Oncorhynchus* spp.) collected with purse seines in marine waters of southeastern Alaska in 1983 and 1984 and northern British Columbia in 1984. Associated prey assemblages were sampled with neuston and plankton nets in 1984. Salmon diets included at least 30 taxa of prey. Crustaceans (principally hyperiid amphipods), fish, and tunicates were the most important prey of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon. Fish were the most important prey of coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon and made up the highest percentage of stomach content weight for all salmon species. Diet shifted from crustaceans in 1983 to fish in 1984 for juvenile pink, sockeye, and chum salmon. Diet overlapped significantly ($\hat{C}_\lambda$>0.60) between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon. Coho salmon diet overlap was <0.60 in all paired comparisons. Nearly all (98.6%) of the 2,210 stomachs examined were at least half full. Although, in general, prey consumed were not very similar to prey observed in the environment, the composition of salmon diets was more similar to neuston collections than to zooplankton collections.

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Fishery Bulletin 96:285–302 (1998).

All Pacific salmon (*Oncorhynchus* spp.) migrate as juveniles from shallow waters near shore to coastal and oceanic feeding areas of the North Pacific Ocean, where species, stocks, and age classes mix (Hartt and Dell, 1986; Ware and McFarlane, 1989; Pearcy, 1992). Substantial evidence suggests that salmon production around the Gulf of Alaska increased dramatically in the late 1970's, possibly owing to enhanced early ocean survival (Pearcy, 1992; Beamish and Bouillon, 1993; Brodeur and Ware, 1995). Increased densities are evident in the commercial harvest of salmon in Alaska; for example, salmon catch reached record numbers in 1993, nearly doubling over 25 years to approach 200 million fish (Wertheimer, 1997). This increase is attributed to several factors, including growing enhancement efforts and environmental conditions that favor survival of both wild and hatchery salmon stocks.

The increase in numbers of subadult and adult salmon feeding in marine waters has prompted interest in possible density-dependent effects on survival, growth, and production of salmon stocks around the Pacific rim (e.g. Helle, 1989; Kaeriyama, 1989; Ishida et al., 1993; Helle and Hoffman, 1995). Fishery managers are concerned about the effects of increasing interactions between salmon populations—both wild and enhanced—in the various marine habitats where they mature (McNeil and Himsworth, 1980; Peterson et al., 1982; Brodeur, 1989; Brodeur and Pearcy, 1990; Pearcy, 1992). The feeding ecology of juvenile salmon is a pertinent, but not well known, topic.

The objective of this study was to describe the feeding habits of juvenile salmon during their first summer in coastal waters of the eastern Gulf of Alaska. Although Hartt and Dell (1986) summarized the distribution, migration, and growth of juvenile salmon in the North Pacific Ocean and the Bering Sea, diet and feeding were addressed superficially. Other references concerning juvenile salmon feeding habits during early marine residence, especially along the open coast, are limited (Pearcy, 1992; Brodeur[1]), and juvenile salmon diets are often

[1] See next page for footnote.

treated as a subset of adult diets (e.g. Groot and Margolis, 1991). Therefore, as a first step to understanding trophic interactions during their first marine summer, our research focused on the feeding habits and diet overlap of juvenile chinook (*O. tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon. We compared diet overlap between species, habitats, months, and years and also examined the similarity of salmon diets with samples of prey collected concurrently.

Methods

Fish collection

Juvenile salmon were collected in 120 purse-seine sets made along transects with two vessels and two seines (Table 1; see also Jaenicke and Celewycz, 1994). The 28-m NOAA RV *John N. Cobb* fished a table seine in the marine waters of southeastern Alaska during August 1983 and July and August 1984 (Fig. 1). The 24-m FV *Bering Sea* fished a drum seine in the open coastal waters of northern British Columbia during July 1984. Purse-seine sets at all locations were standardized to compensate for different sizes, meshes, and areas enclosed; both nets had 25-mm mesh in the bunt (Jaenicke and Celewycz, 1994). Each station was fished only once during a period, except on a few occasions when a set was repeated following an empty haul. Fishing was conducted almost exclusively between 0600 and 1800 hours. All sets were round hauls (i.e. the seine was not towed or held open to increase catches). The distribution, size, and abundance of juvenile salmon examined for our study have been summarized in a companion paper by Jaenicke and Celewycz (1994).

The waters sampled were partitioned into discrete habitats: 1) outside waters: the open waters adjacent to the Gulf of Alaska; 2) inside waters: the enclosed marine waters of the Alexander Archipelago; and 3) protected outer-coast inlets (Fig. 1). Outside waters were further partitioned into nearshore (0–37 km offshore) and offshore (46–74 km offshore) during August 1984; seining was restricted to within 37 km of shore during other sampling periods. Inside waters were partitioned into bays and passages (connecting to the Gulf of Alaska). Sampling in outside waters was along transects about 72 km apart in southeastern Alaska and 108 km apart in British Columbia. Transects began as close to shore as submarine topography and seine depth permitted and continued up to 74 km offshore, depending on fish abundance and weather.

Fish from each purse-seine haul were anesthetized with MS 222 (tricaine methanesulfonate), sorted, identified, and measured on board the vessel. A subsample of each salmon species ($n \leq 25$) was preserved in 10% formalin-seawater solution for later stomach analysis (Table 1). Nonsalmonids caught incidentally were identified and enumerated, catch per unit of effort (CPUE) was estimated, and a subsample was measured for length as part of prey assemblage assessments (see below). Sea surface temperature (SST) to the nearest 0.2°C was recorded at every purse-seine site.

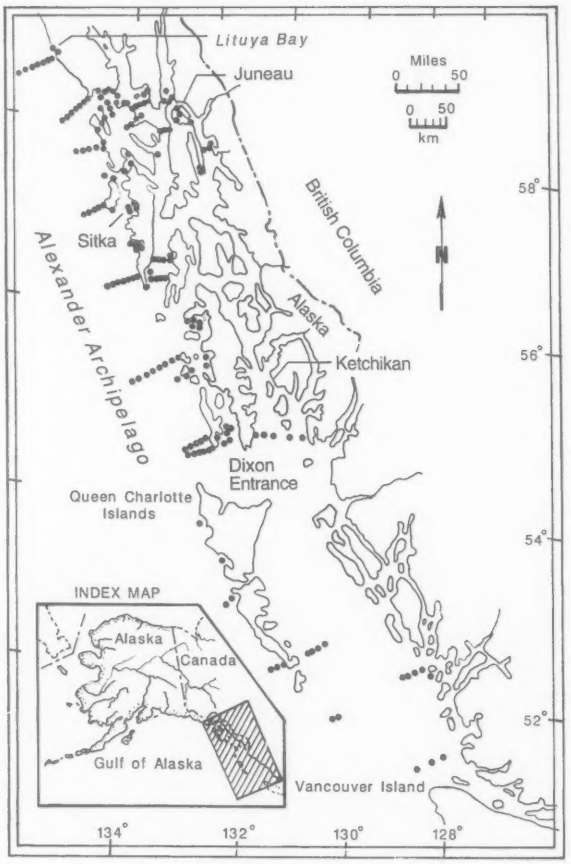

Figure 1

Location of purse-seine sets in southeastern Alaska in 1983 and 1984 and in British Columbia in 1984.

[1] Brodeur, R. D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific (INPFC Doc.) FRI-UW-9016. Fish. Res. Inst., Univ. Washington, Seattle, 38 p.

Table 1

Number of purse-seine sets by time period and habitat and subsample size by species of juvenile salmon used in diet analyses. BC = British Columbia; AK = Alaska.

Habitat	Number of sets	Number of sets catching juvenile salmon	Number of fish				
			Pink	Chum	Sockeye	Coho	Chinook
August 1983							
Inside inlet	15	3	21	23	2	14	1
Inside passage	39	23	142	112	44	88	2
Outer coast inlet	27	8	60	47	0	21	0
Outside waters	8	4	15	2	9	26	0
Total	89	38	238	184	55	149	3
July 1984							
Inside inlet	13	5	14	17	12	63	10
Inside passage	5	2	20	3	9	44	0
Outer coast inlet	14	5	8	3	0	28	0
Outside waters (BC)	21	11	69	30	55	7	3
Outside waters (AK)	33	15	94	40	83	27	1
Total	86	38	205	93	159	169	14
August 1984							
Inside inlet	18	6	35	16	10	82	6
Inside passage	19	7	61	10	5	73	10
Outer coast inlet	4	1	0	12	0	3	0
Outside nearshore	26	20	183	97	80	55	5
Outside offshore	11	10	93	41	52	12	0
Total	78	44	372	176	147	225	21
All periods combined							
Inside inlet	46	14	70	56	24	159	17
Inside passage	63	32	223	125	58	205	12
Outer coast inlet	45	14	68	62	0	52	0
Outside waters	99	60	454	210	279	127	9
Total	253	120	815	453	361	543	38

Stomach analysis

Each fish was weighed to the nearest milligram and measured to the nearest millimeter fork length (FL) in the laboratory. Stomachs were excised and placed in 70% isopropyl alcohol. During analysis, stomach fullness on a scale of 0–6 (0=empty, 6=distended) and digestion on a scale of 1–4 (1=fresh prey items, 4=completely digested) were visually estimated. Stomach contents were weighed, and prey items were separated, identified to the lowest convenient taxon, and counted. Up to 100 individuals of each prey category that had been removed in good condition from the stomach were used to measure initial wet weights. Prey fish in an advanced state of digestion were assigned to discrete weight categories based on the most complete specimens encountered: small (estimated 6.0 mg), medium (184.4 mg), and large (580.5 mg). Dry weights were obtained by drying the samples in an oven at 60°C until constant weights were obtained.

Sampling and analysis of prey assemblages

Prey assemblages were sampled with neuston and plankton nets in the areas fished in 1984. Neuston collections were made with a rectangular 100 × 35-cm-opening neuston-net frame containing a conical 505-µm-mesh net; tows were made at 45 of 54 outside-water locations, 7 of 14 outer-coast-inlet locations, and 5 of 18 inside-water locations. The neuston net was towed horizontally, half-submerged, so that it sampled the water column from the surface to approximately 17 cm depth (Brodeur, 1989; Brodeur[2]). The plankton collections were made with a 70-cm diameter conical plankton net of 303-µm mesh; tows were made along purse-seine transects at four 4-km locations and six 16-km locations in

[2] Brodeur, R. D., W. G. Pearcy, B. C. Mundy, and R. W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution, and utilization by juvenile salmonids. Oregon State Univ. Publ. ORESU-T-87-001, 61 p.

outside waters, and at six locations in inside waters. All plankton tows were oblique from the surface to a depth of 50 m. Samples were preserved in a 10%-formalin-seawater solution after debris was removed.

Plankton and neuston samples were sorted to remove large organisms, such as gelatinous zooplankton. We then split the sample with a Folsom splitter until a subsample of about 500 organisms remained. Plankton organisms were identified to the lowest convenient taxon and counted. Detailed composition of many of the neuston samples has been presented elsewhere (Brodeur[2]).

Data analysis

Stomach data were partitioned into subsets according to salmon species, geographic area, habitat, distance offshore, month, and year. The index of relative importance (IRI; Pinkas etal., 1971) was calculated for each data subset. The modified IRI (dry weight rather than volume) was used to characterize the diet of each species and to rank prey taxa:

$$IRI = (N + W)F,$$

where N is numerical percentage, W is weight percentage, and F is frequency of occurrence (FO) percentage. In all comparisons, the IRI is expressed as a percentage of total IRI for each data subset.

Morisita's index of overlap as modified by Horn (1966) was used to calculate overlap between species pairs; values range from 0 (no overlap) to 1 (complete overlap):

$$\hat{C}_\lambda = \frac{2\sum_{i=1}^{S} x_i y_i}{\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2},$$

where x_i and y_i are proportions of the numbers of individuals of prey species i found in the predator species x and y, respectively.

The percent similarity index (PSI; Whittaker, 1975) was used to compare stomach samples to plankton samples:

$$PSI = \sum \min(p_a \text{ or } p_b),$$

where p_a is percentage number for a given species in sample A, and p_b is percentage number for the same species in sample B. A PSI value of 1.00 shows complete similarity; a value of 0 indicates no similarity. We considered values ≥0.60 to be significant for both overlap indices. Chinook salmon were not included in the analysis of overlap because of small sample sizes (Table 1). Following Brodeur and Pearcy (1990), we tested for differences in the occurrence of principal prey between years, months, areas, and distance offshore using χ^2.

We examined data for neuston and plankton prey samples collected at locations where stomachs of at least five specimens of one salmon species were available and included a taxon in the prey collections. To measure prey selection, we used Strauss's linear food selection index (Strauss, 1979):

$$L = r_i - p_i,$$

where r_i and p_i are the proportional abundances of prey item i in the gut and habitat, respectively. Selection values range from –1, indicating avoidance or negative accessibility, to +1, indicating preference or positive selection; 0 indicates random feeding. Values are extreme only when the prey item is proportionately abundant but rarely consumed (–1), or is proportionately rare but consumed almost exclusively (+1). We tabulated selection values >0.10 or <–0.10 for an indication of the positive or negative selection of a particular taxon.

To compare the number of stomachs required to characterize the breadth of diet for each species of salmon, we pooled the stomachs over all periods and habitats. Stomachs were selected randomly, and the cumulative number of taxa were plotted versus the number of stomachs until the asymptote was reached (Hurtubia, 1973).

Results

Description of diet

All salmon species The prey spectrum for juveniles of five Pacific salmon species comprised at least 30 taxa (Table 2). The six taxonomic groups of greatest importance (IRI) were calanoid copepods, hyperiid amphipods, euphausiids, decapods, tunicates, and fishes (Table 3). In pooled samples, fish were the most important prey for coho and chinook salmon (IRI=63.8% and 76.4%) but were only moderately important for the other species (IRI 28.3–40.3%). Hyperiid amphipods, most commonly *Themisto* spp., were also important prey for pink, chum, and sockeye salmon (IRI 28.0–39.6%). However, the biomass of teleost prey made up more than 75% of the total biomass consumed by each of the juvenile salmon species in pooled samples.

The full breadth of the prey spectrum for juvenile salmon species was obtained by randomly selecting

16–95% of the actual number of stomachs analyzed (Fig. 2). The highest cumulative numbers of prey taxa (n=25 and 26, respectively) were observed after we had randomly subsampled 86 coho and 396 pink salmon stomachs (Fig. 3). Virtually all chinook salmon analyzed (39) were needed to reach the 14 cumulative prey taxa observed. The curves of cumulative number of taxa for pink and chum salmon were more similar than for any other pair of species (Fig. 3).

Pink salmon The prey of juvenile pink salmon (85–222 mm FL; $\bar{x}$=142 mm; SD=22.9) encompassed 26 taxa and several life-history stages. Hyperiid amphipods, especially the genus *Themisto*, had the highest total IRI (Fig. 4) and highest FO and mean abundance over all periods and habitats (Table 3). Juvenile fish had the second-highest IRI and the greatest biomass—76% of pooled weight of stomach contents. In 1984, the IRI for fish prey did not rank first, but it was more than twice the 1983 value; fish prey ranked higher in Alaska than in British Columbia. Tunicates, primarily the larvacean *Oikopleura dioica*, were the third most important prey in pooled samples.

Chum salmon The prey spectrum for juvenile chum salmon (80–276 mm FL; $\bar{x}$=151 mm; SD=28.4) included 22 taxonomic groups and several life-history stages. Juvenile fish, tunicates (salps and the larvacean *O. dioica*), and hyperiid amphipods (*Themisto* spp.) had the highest IRI's overall (Fig. 5).

Sockeye salmon The prey spectrum for juvenile sockeye salmon (91–202 mm FL; $\bar{x}$=151 mm; SD=18.9) encompassed 18 taxonomic groups and several life-history stages. Fish prey had the highest IRI (40.3%) and the greatest average weight (87.2%) pooled over all habitats and periods (Table 3; Fig. 6), although no fish were sampled from outer-coast inlets (Table 1). Fish prey were more important in 1984 than in 1983, especially in the outside waters of southeastern Alaska in July 1984 and inside inlets and outside waters (>37 km) in August 1984 (Fig. 6). Hyperiid amphipods (*Themisto* spp.) were the second

Table 2

Prey from juvenile salmon stomachs as index of relative importance (IRI). $IRI = (N + W)FO$, where N= numerical percentage, W = weight percentage, and FO = frequency of occurrence percentage. Numbers in parentheses are totals of taxonomic groups for which more than one taxon is listed.

	IRI (%)				
Prey	Pink	Chum	Sockeye	Coho	Chinook
Polychaeta					
Unidentified	<0.01	<0.01	—	<0.01	<0.01
Mollusca	(0.90)	(0.16)	(0.17)	(0.02)	(—)
Gastropoda					
Limacina helicina	0.82	0.16	0.15	0.02	—
Bivalvia					
Unidentified	<0.01	<0.01	—	—	—
Cephalopoda					
Unidentified	0.08	<0.01	0.02	<0.01	0.18
Copepoda	(3.71)	(2.93)	(4.15)	(0.02)	(<0.01)
Neocalanus cristatus	<0.01	—	—	—	—
Epilabidocera longipedata	<0.01	—	<0.01	—	—
Unidentified	3.70	2.93	4.14	0.02	<0.01
Cumacea					
Unidentified	<0.01	<0.01	—	—	—
Amphipoda					
Hyperiidea	(39.61)	(28.03)	(36.48)	(6.84)	(0.10)
Hyperia sp.	0.01	0.01	0.01	0.02	0.01
Themisto spp.	38.75	27.44	36.11	6.73	0.08
Primno macropa	0.83	0.58	0.36	0.09	0.01
Vibilia sp.	0.02	<0.01	0.01	<0.01	—
Euphausiacea	(5.95)	(6.18)	(12.62)	(3.88)	(18.34)
Euphausia pacifica	<0.01	—	—	<0.01	—
Thysanoessa spinifera	<0.01	0.01	—	0.01	0.08
Unidentified	5.94	6.17	12.62	3.86	18.26
Decapoda					
Unidentified	4.67	3.16	3.64	25.26	4.81
Insecta					
Unidentified	0.01	<0.01	<0.01	0.01	—
Chaetognatha					
Unidentified	0.01	0.01	<0.01	<0.01	—
Urochordata					
(tunicates)	(13.56)	(30.32)	(2.26)	(0.03)	—
Salpidae					
Unidentified	<0.01	0.21	—	<0.01	—
Larvacea					
Oikopleura dioica	13.56	30.11	2.26	0.03	—
Osteichthyes	(31.11)	(29.88)	(40.27)	(63.78)	(76.42)
Clupea pallasi	—	—	—	0.01	0.26
Osmeridae	<0.01	0.02	—	<0.01	0.61
Myctophidae	0.02	0.02	<0.01	—	—
Theragra chalcogramma	—	—	—	0.01	—
Sebastes spp.	0.04	—	0.03	0.04	—
Cottidae	—	—	—	<0.01	—
Stichaeidae	<0.01	—	<0.01	<0.01	0.02
Ammodytes hexapterus	<0.01	0.03	—	0.30	0.47
Pleuronectidae	—	<0.01	<0.01	0.02	—
Unidentified	31.04	29.80	40.22	63.39	75.06

Table 3

Stomach contents of juvenile salmon in marine waters of southeastern Alaska and northern British Columbia in 1983 and 1984. *N* is numerical percentage, *W* is dry weight percentage, *FO* is frequency of occurrence percentage of fish with prey item *i*, and *IRI* is percent of total IRI for all prey taxa. $IRI = (N + W)FO$. Taxa are omitted if IRI is ≤1% for all salmon.

	Pink salmon				Chum salmon				Sockeye salmon				Coho salmon				Chinook salmon			
	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)
All periods combined																				
Calanoids	5.6	0.9	47.9	3.7	5.4	0.8	32.9	3.0	9.0	0.5	41.5	4.2	—	—	—	—	—	—	—	—
Decapods	3.8	4.0	48.6	4.7	2.4	3.6	36.6	3.1	5.4	2.6	43.2	3.6	52.0	0.1	56.3	25.3	11.2	0.2	38.5	4.8
Euphausiids	5.2	5.5	46.2	6.0	6.0	5.9	39.8	6.1	16.5	4.3	57.4	12.6	12.8	0.1	35.8	3.9	52.6	0.2	33.3	18.3
Hyperiids	45.2	5.8	90.3	39.6	29.5	5.7	73.6	28.0	46.2	3.7	90.1	36.5	22.9	0.1	46.4	6.8	1.5	0.2	7.7	0.1
Tunicates	32.2	0.1	35.2	13.6	52.5	0.1	46.7	30.1	16.4	<0.1	13.1	2.3	—	—	—	—	—	—	—	—
Teleosts	1.3	76.0	39.1	31.2	0.9	82.7	28.6	28.3	2.9	87.2	47.0	40.3	8.4	99.5	73.2	63.8	30.2	99.0	71.8	76.4
Total	93.3	92.3		98.8	96.7	98.7		98.6	96.4	98.3		99.5	96.1		99.8	99.8	95.5		99.5	99.6
August 1983																				
Calanoids	6.4	2.9	62.6	6.6	2.0	4.7	39.7	3.1	10.9	4.6	52.7	6.0	0.4	<0.1	10.1	<0.1				
Decapods	4.3	8.6	60.9	8.9	0.9	12.1	32.6	4.8	1.1	8.3	30.9	2.2	46.4	0.5	63.1	26.4				
Euphausiids	4.9	14.1	52.9	11.4	5.3	32.7	46.2	18.4	17.0	39.0	76.4	31.5	5.8	0.6	36.9	2.0				
Hyperiids	37.0	12.4	71.0	33.6	31.5	28.0	64.7	38.5	58.5	30.7	94.5	55.1	41.5	0.6	59.7	21.7				
Tunicates	38.7	0.2	48.7	20.3	56.8	0.5	60.9	28.8	8.7	0.1	14.5	0.9	0.1	<0.1	6.0	<0.1				
Teleosts	0.4	56.7	29.9	16.6	0.2	20.2	19.6	4.6	0.3	16.7	21.8	2.7	2.7	96.4	61.1	49.1				
Total	91.7	94.9		97.4	96.7	98.2		98.2	96.5	99.4		98.4	96.9		98.1	99.2				
July 1984																				
Calanoids	15.0	0.8	39.0	7.3	23.4	1.4	28.0	11.0	12.1	0.4	4.3	5.6	0.7	<0.1	7.1	<0.1				
Decapods	4.7	1.9	42.0	3.3	1.1	2.1	26.9	1.4	8.8	0.8	32.1	3.2	54.3	0.1	65.7	27.6				
Euphausiids	7.0	5.0	46.3	6.6	4.8	8.1	37.6	7.7	23.0	3.4	62.3	17.0	16.6	0.1	33.7	3.8				
Hyperiids	45.2	4.3	68.3	39.4	26.0	6.3	53.8	27.1	37.8	2.0	70.4	28.9	6.1	0.1	25.4	0.8				
Tunicates	11.9	<0.1	17.6	2.5	34.3	0.1	29.0	15.8	9.1	<0.1	7.5	0.7	4.1	<0.1	5.3	<0.1				
Teleosts	3.6	84.2	39.0	38.4	3.9	77.4	32.3	35.0	4.2	92.0	45.9	43.9	15.5	99.7	84.0	67.6				
Total	87.4	96.2		97.5	93.5	95.4		98.0	95.0	98.6		99.3	97.3		100	99.8				
August 1984																				
Calanoids	2.3	0.7	37.9	1.3	3.8	0.3	25.1	1.5	4.7	0.5	32.7	1.8	0.2	<0.1	2.7	<0.1				
Decapods	3.2	3.9	43.4	3.7	5.0	2.9	42.9	5.0	4.5	5.3	61.2	6.4	58.3	0.1	42.7	24.7				
Euphausiids	4.8	3.7	39.3	3.9	7.3	2.4	29.7	4.2	9.6	3.8	41.5	5.9	19.7	0.1	32.4	6.3				
Hyperiids	50.1	5.0	65.3	40.8	27.9	3.0	53.1	22.6	47.5	5.1	68.7	36.5	10.3	0.1	24.0	2.1				
Tunicates	34.4	<0.1	34.7	14.4	52.8	<0.1	37.1	28.9	28.3	<0.1	19.7	5.9	<0.1	<0.1	0.1	<0.1				
Teleosts	1.1	85.1	38.5	35.5	0.8	90.8	28.0	37.3	3.1	83.1	47.6	43.4	10.7	99.6	72.9	66.8				
Total	95.9	98.4		99.6	97.6	99.4		99.5	97.7	97.8		99.9	99.2		99.9	99.9				

most important prey group (IRI=36.5%) and had the highest FO and average count (Table 3).

Coho salmon The prey spectrum of juvenile coho salmon (112–309 mm FL; $\bar{x}$=222 mm; SD=35.1) encompassed 25 taxonomic groups, including eight identifiable fish families (Table 2). Teleosts made up 99.5% of the total prey weight, with a mean number of 8.4 fish consumed by 73.2% of the coho predators (Table 3). Juvenile fishes were the principal component of coho salmon diet in all habitats except in the outside waters during August 1983 (Fig. 7), when decapod larvae were more important (IRI=66%). The IRI for prey fish ranged from 51% to 81% in the other habitats, with Pacific sand lance (*Ammodytes hexapterus*) the most prevalent species. Other identifiable prey fish (in order of importance) included walleye pollock (*Theragra chalcogramma*), rockfish (*Sebastes* spp.), flatfish (Pleuronectidae), Pacific herring (*Clupea pallasi*), smelt (Osmeridae), pricklebacks (Stichaeidae), and sculpins (Cottidae). Fish were more important in 1984 than in 1983 and higher in Alaska than in British Columbia.

Chinook salmon The prey spectrum of juvenile chinook salmon (139–324 mm FL; $\bar{x}$=224 mm; SD=58.4) encompassed 14 taxonomic categories and four identifiable fish families (Table 2). Fish were the most important prey: IRI's ranged from 28% to 100% among habitats (data not shown). Fish made up 99% (biomass) of chinook salmon stomach contents in pooled samples, with a mean of 30.2 individuals con-

sumed by approximately 72% of the predators (Table 3). Identifiable fish (in order of importance) included smelt, Pacific sand lance, Pacific herring, and pricklebacks. Euphausiids were an important prey principally in inside inlets during July 1984. Incidental prey included decapod larvae, squid, and hyperiid amphipods.

Variation in principal prey

Diets of all four species varied greatly (Table 4). Variation in the FO of the six principal prey (calanoids, decapod larvae, euphausiids, fish, hyperiid amphipods, and tunicates) was greatest when compared between years: the FO of most invertebrate taxa decreased significantly ($P \leq 0.05$) in the diets from August 1983 to August 1984, whereas the FO of teleost prey increased (Tables 3 and 4). Except for coho salmon, variation in the FO of fish was greatest for inshore-offshore comparisons; significantly more fish were consumed by the other species offshore (>37 km from the coast) than inshore (0–37 km from the coast) (Table 4; $12.69 < \chi^2 < 47.72$; $P \leq 0.001$). In 1984, the FO of two principal prey taxa differed consistently in opposite directions between areas: pink, chum, and sockeye salmon ate teleost prey significantly less often ($6.94 < \chi^2 < 13.42$; $P \leq 0.01$), whereas all four species consumed euphausiids significantly more often ($5.66 < \chi^2 < 17.13$; $P \leq 0.05$) in British Columbia waters than in Alaska. The diet of sockeye salmon varied more than that of the other species between years (August 1983 and August 1984), months (July and August), and areas (British Columbia and southeastern Alaska; Table 4).

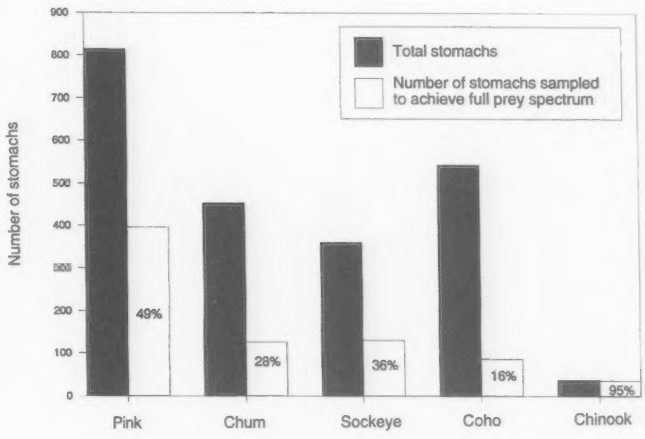

Figure 2

Total number of stomachs sampled for five species of juvenile Pacific salmon and number and percentage of randomly selected stomachs, from samples pooled over habitats and time periods, which were required to achieve the full prey spectrum for each species as defined in this study.

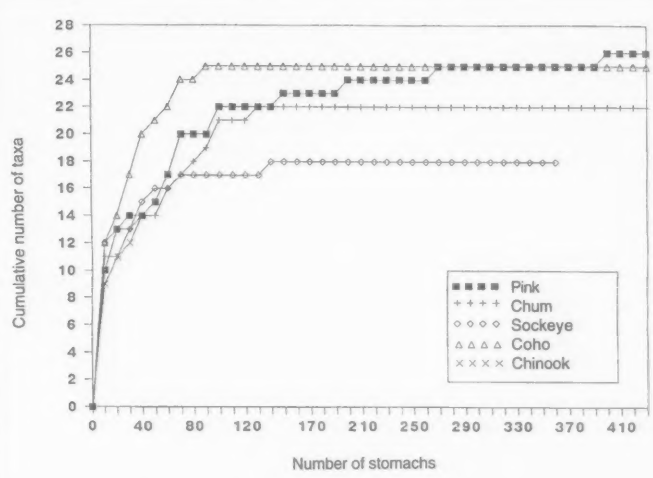

Figure 3

Curves of cumulative number of prey taxa versus pooled number of fish examined from five Pacific salmon species in marine waters of southeastern Alaska and northern British Columbia.

Diet overlap

Samples pooled over time and habitat Significant diet overlap ($\hat{C}_\lambda > 0.60$) was found between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon when all samples were pooled. Coho salmon diet overlap was less than 0.60 in all comparisons. Diet overlap was not calculated for chinook salmon because of small sample sizes (Table 1). The greatest diet overlap was between pink and sockeye salmon juveniles ($\hat{C}_\lambda = 0.93$; Table 5); both species ate fish and hyperiid amphipods. The second-greatest diet overlap ($\hat{C}_\lambda = 0.91$) was between pink

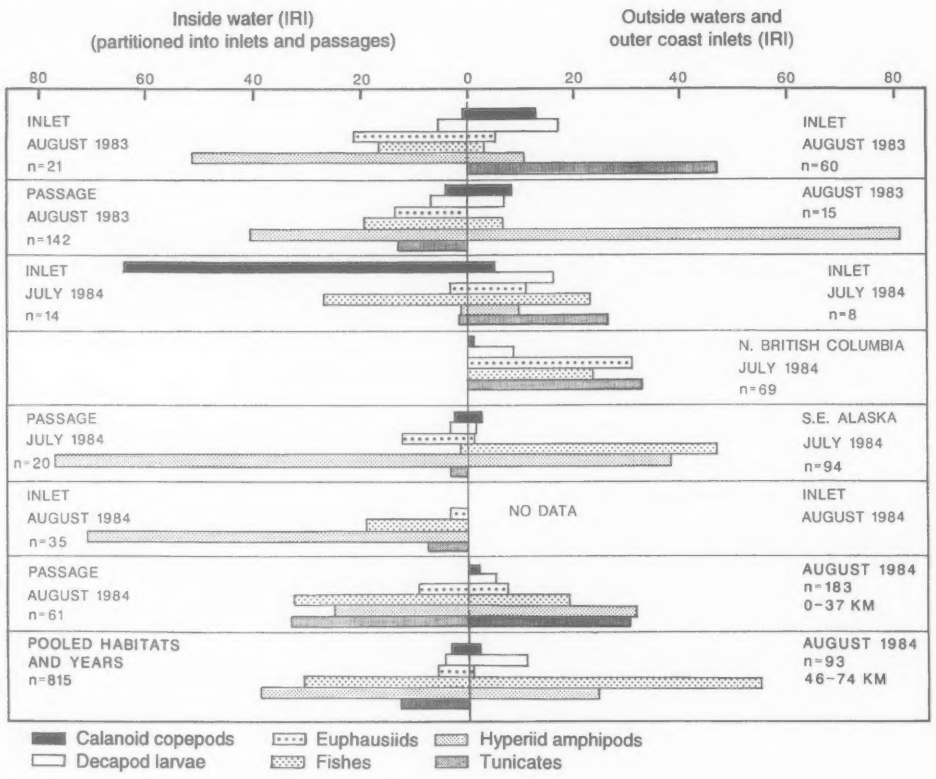

Figure 4

Index of relative importance (IRI) of principal prey of juvenile pink salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

and chum salmon; both ate hyperiid amphipods, fish, and *Oikopleura dioica*. The third-highest diet overlap in all pooled samples was between chum and sockeye salmon ($\hat{C}_\lambda$=0.73); both species consumed fish, hyperiid amphipods, and euphausiids.

Temporal diet overlap The degree of diet overlap among salmon species pairs varied by time period when habitat was not considered. In August 1983, diet overlap, based on the consumption of hyperiid amphipods, was greatest for pink and chum salmon juveniles ($\hat{C}_\lambda$=0.95; Table 5), *O. dioica*, and euphausiids. Diets of juvenile pink and sockeye salmon overlapped significantly ($\hat{C}_\lambda$=0.72) on the basis of hyperiid amphipods and euphausiids. A lesser, but still significant, diet overlap ($\hat{C}_\lambda$=0.62) occurred between sockeye and coho salmon on the basis of hyperiid amphipods, decapod larvae, and fish.

Diet overlap was lower in July 1984, when samples included waters outside of British Columbia, than in August 1984. Diet overlap was significant for combinations of pink, chum, and sockeye salmon, but not for combinations including coho salmon (Table 5). The greatest overlap occurred between pink and chum salmon ($\hat{C}_\lambda$=0.80), pink and sockeye salmon ($\hat{C}_\lambda$=0.79), and chum and sockeye salmon ($\hat{C}_\lambda$=0.73), which was principally due to similar proportions of hyperiid amphipods and juvenile fish. The relative importance of larvaceans accounted for the greatest difference in the diets of these three species: *O. dioica* made up nearly 20% of the IRI for chum salmon, compared with less than 3% for pink and sockeye salmon.

In August 1984, the diets of pink, sockeye, and chum salmon overlapped greatly, whereas coho salmon diet did not overlap with that of any other species (Table 5). Diets of pink and sockeye salmon overlapped almost

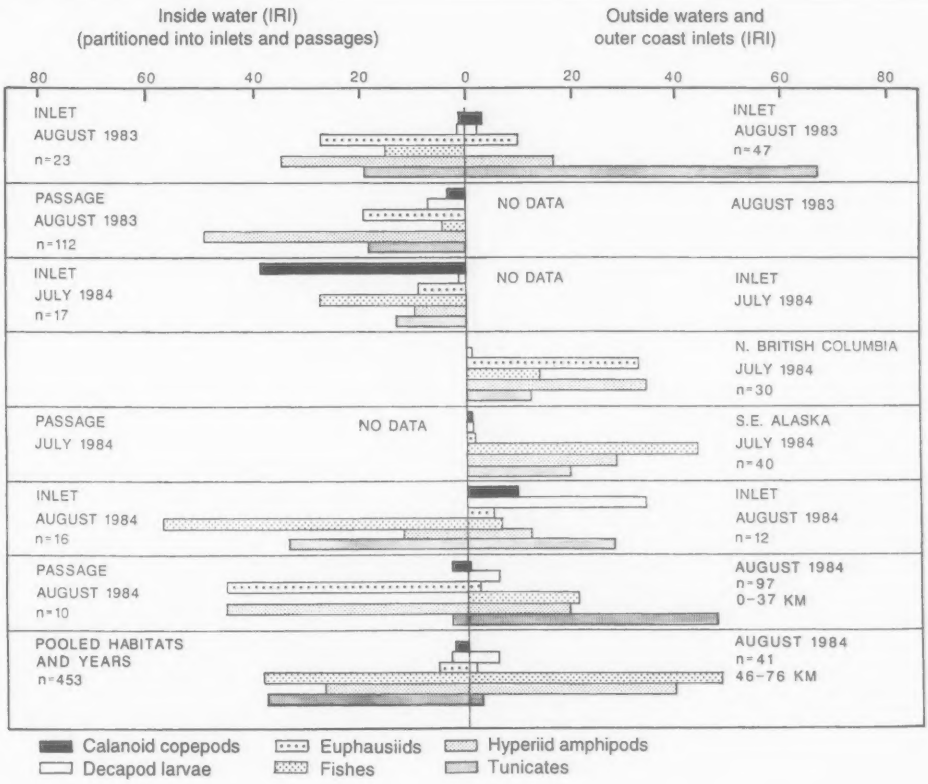

Figure 5

Index of relative importance (IRI) of principal prey of juvenile chum salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

completely ($\hat{C}_\lambda$=0.99); prey composition and IRI for each prey category were highly similar (Table 2). Pink and chum salmon diets ($\hat{C}_\lambda$=0.88) and sockeye and chum salmon diets ($\hat{C}_\lambda$=0.85) had almost identical prey species compositions, although proportions of prey categories differed (Table 2).

Spatial diet overlap Diet overlap was more common for species comparisons in outside waters than in inside waters. Of all possible habitat comparisons, diet overlap was significant ($\hat{C}_\lambda \geq 0.60$) in 42% of the outside-waters comparisons, 39% of inside-passage comparisons, and 29% of inside-inlet comparisons (Table 5). Within each habitat, mean overlap (all periods) was significant in inside inlets for pink and chum salmon ($\hat{C}_\lambda$=0.66), inside passages for pink and chum salmon ($\hat{C}_\lambda$=0.91), and chum and sockeye salmon ($\hat{C}_\lambda$=0.73), and outside waters for pink and sockeye salmon ($\hat{C}_\lambda$=0.83), chum and sockeye salmon ($\hat{C}_\lambda$=0.68), and pink and chum salmon ($\hat{C}_\lambda$=0.67).

Fullness and digestion

Most salmon stomachs were evaluated to be at least half full (fullness index of 3); coho salmon stomachs were more full than those of other species (Table 6). Stomach fullness was always greater for fish from the inside waters than from outside waters; stomachs of fish caught 0–37 km offshore were less full than those of fish caught >37 km offshore. Only 32 of 2,210 (1.4%) stomachs sampled were empty: 72% in outside waters, 3% in coastal inlets, and 25% in inside waters. The contents of most stomachs were "partly digested" (digestion index of 2). Pink, chum, and coho salmon from inside waters had stomach contents in an earlier stage of digestion than fish

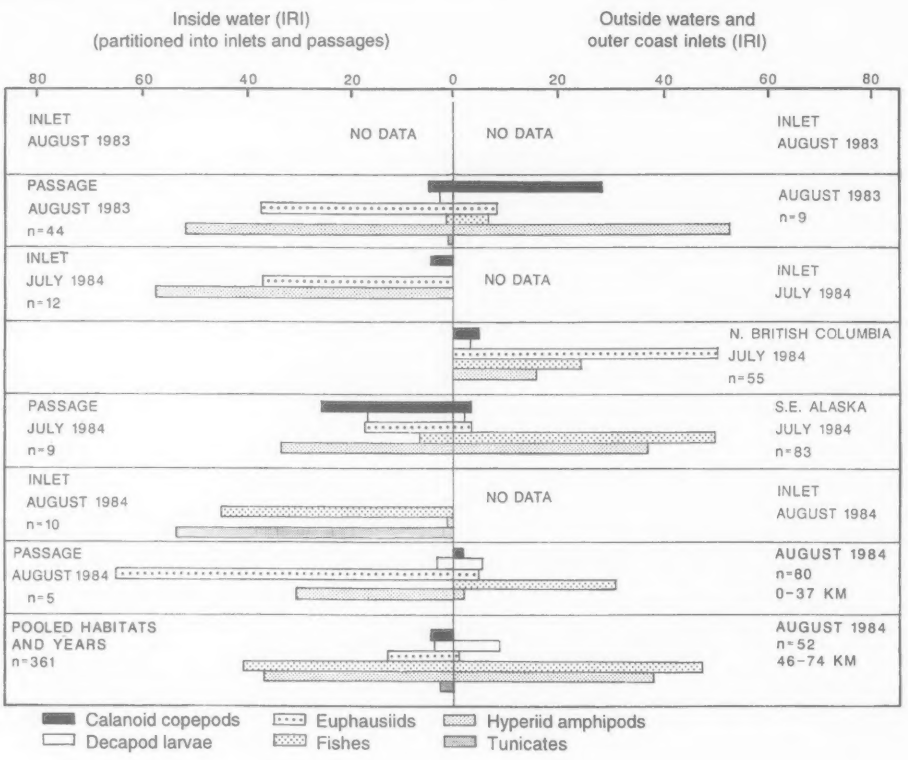

Figure 6

Index of relative importance (IRI) of principal prey of juvenile sockeye salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

from outside waters; the reverse was observed for sockeye salmon.

Salmon diet and the prey assemblages

Neuston samples from the outside waters of British Columbia and southeastern Alaska included 13 and 14 major taxa, respectively (Table 7). In British Columbia, decapod larvae made up 83% of the number of prey, hyperiid amphipods 12%, calanoid copepods 4%, and all other taxa <1%. Prey diversity of neuston samples was more even for southeastern Alaska than for British Columbia; half of the 14 taxa represented ≥2% of the total abundance. In Alaska, calanoid copepods were the most abundant organism (59% of the total), decapod larvae were second (21%), and gammarid amphipods were third (9%). The density of neustonic organisms was about five times greater in samples from British Columbia than in those from southeastern Alaska.

In zooplankton samples, the number of individuals and dominant taxa differed with time and habitat (Table 7). Zooplankton abundance in outside waters was about twice that of inside waters of southeastern Alaska in July 1984. Calanoid copepods were the dominant organisms in the samples (90% of total abundance).

The PSI indicated little relationship between prey consumed by salmon and prey available in the environment (Table 8). Neuston samples were generally more similar to salmon diet than were zooplankton samples. Similarity for the neuston samples ranged from 0% to 37.8% and averaged from 9.1% for sockeye salmon to 16.7% for coho salmon (Table 8). The PSI values for the plankton samples ranged from 0.2% to 24.9% and averaged from 2.2% for chum salmon to 9.3% for sockeye salmon.

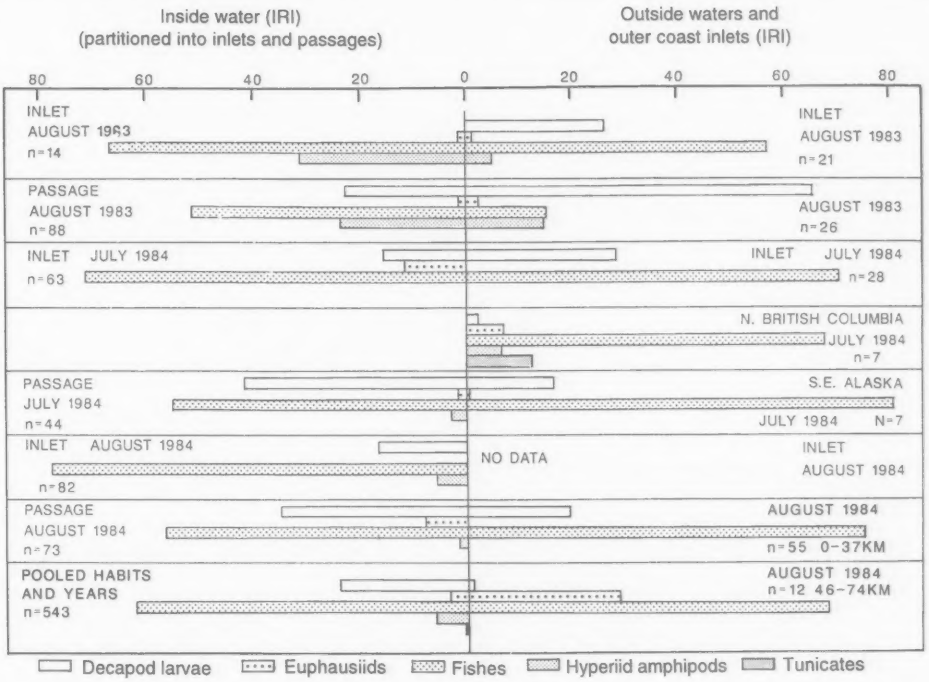

Figure 7

Index of relative importance (IRI) of principal prey of juvenile coho salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

We examined patterns of prey selectivity by applying Strauss's linear index of food selection to the same sets of predator-prey samples that had been analyzed for similarity. Pink and sockeye salmon selected ($L>0.10$) neustonic prey more often than planktonic prey, and neustonic hyperiid amphipods were the most frequently selected organism. Chum and coho salmon selected neustonic and planktonic prey in nearly equal frequencies (Table 9). All salmon species avoided ($L<-0.10$) neustonic decapod larvae. Selection patterns for planktonic prey varied more than for neustonic prey; however, salmon generally selected planktonic decapod larvae, hyperiid amphipods, euphausiids, and fishes and avoided the proportionately more abundant calanoid copepods.

Discussion

This study of the food habits of five sympatric species of Pacific salmon during their first summer in the marine waters of southeastern Alaska and northern British Columbia is the first detailed study for this geographic area. Feeding patterns were dynamic, with shifts in the important prey categories between salmon species, years, and areas.

We analyzed the importance of two major prey categories, zooplankton and teleosts, and examined data for temporal and spatial shifts in feeding patterns among salmon species. First, in pooled samples (all periods and habitats), zooplankton were much more important in pink, chum, and sockeye salmon diets (60–70% IRI) than in coho and chinook salmon diets (36% and 24% IRI; Table 3). When the two years of data were analyzed separately, however, contrasting patterns emerged. In 1983 (August), pink, chum, and sockeye salmon were mostly planktivorous (83–97% IRI), and zooplankton IRI was over 50% even for coho salmon. In 1984 (July and August), the proportional number, weight, and FO of teleost prey increased in diets of all salmon species; however, whereas zooplankton remained most important in the diets of pink,

chum, and sockeye salmon (56–65% IRI), teleosts were most important in coho salmon diets (68%IRI).

Spatial factors that influence both predator and prey, especially latitude and proximity to shore, may account for similarities or differences in principal prey (Andrievskaya, 1970; Brodeur and Pearcy, 1990). Most species of salmon are opportunistic and feed on a wide variety of prey (Beacham, 1986; Brodeur[1]), but their diets are commonly composed of a few taxa readily available at a given time and location. The importance of zooplankton in the diets of juvenile pink, sockeye, and chum salmon in our study is similar to results reported in other studies from the eastern Gulf of Alaska (Manzer, 1969; Jaenicke et al., 1984; Hartt and Dell, 1986), the Sea of Okhotsk (Andrievskaya, 1968, 1970), and other regions of the northeastern Pacific Ocean (Peterson et al., 1982; Brodeur, 1989; Brodeur and Pearcy, 1990). We found that hyperiid amphipods were especially important in pink and sockeye salmon diets, and less so in chum salmon diets. The principal hyperiid amphipod found in diets of these species in the northeastern Pacific Ocean, Iincluding our study, was *Themisto pacifica*. In the more southern latitudes of coastal Washington and Oregon, another hyperiid amphipod (*Hyperoche medusarum*) is an important component in chum, coho, chinook, and sockeye salmon diets (Brodeur and Pearcy, 1990). In that area, however, euphausiids are more important in juvenile chum diets and, to a lesser extent in juvenile coho and chinook salmon diets, than are hyperiid amphipods (Peterson et al., 1982; Brodeur and Pearcy, 1990). Similarly, we found that euphausiids occurred less frequently and were less important in diets of all juvenile salmon located off southeastern Alaska, a downwelling region, compared to diets of salmon from southern British Columbia to Oregon, where upwelling is more prevalent (Ware and McFarlane, 1989).

Table 4

Chi-square (χ^2) values for variation in frequency of occurrence of principal prey in four species of juvenile salmon. Comparisons were made between years (August 1983 and August 1984), months (July 1984 and August 1984), area (northern British Columbia and southeastern Alaska), and distance offshore (0–37km vs. 46–76km). No asterisk indicates $P > 0.05$. * = $P \leq 0.05$; ** = $P \leq 0.01$; and *** = $P \leq 0.001$.

	χ^2			
Taxon	Between years	Between months	Between areas	Between inshore and offshore
Pink salmon				
Calanoids	35.29***	0.07	2.47	0.35
Decapods	18.41***	0.07	1.82	13.04***
Euphausiids	11.35***	2.90	17.13***	3.86*
Hyperiids	2.34	0.62	1.18	8.60***
Tunicates	7.13**	19.48***	6.08*	13.83***
Teleosts	6.39*	0.00	7.33**	47.72***
Chum salmon				
Calanoids	8.62***	0.25	6.08*	0.37
Decapods	4.02*	6.63*	2.04	5.94*
Euphausiids	9.06***	1.74	5.66*	5.15*
Hyperiids	4.93*	0.01	0.12	15.30***
Tunicates	3.78	1.77	3.43	1.36
Teleosts	3.53	0.53	6.94**	26.46***
Sockeye salmon				
Calanoids	6.84**	3.73	3.72	0.08
Decapods	14.77***	26.12***	1.74	1.36
Euphausiids	19.47***	13.21***	14.81***	0.68
Hyperiids	73.17***	57.10***	0.34	0.04
Tunicates	0.72	9.77***	5.45*	4.51*
Teleosts	11.05***	0.09	13.42***	12.69***
Coho salmon				
Calanoids	9.26***	4.35*	—	—
Decapods	14.96***	20.50***	0.00	1.46
Euphausiids	0.80	0.07	7.20**	3.98*
Hyperiids	48.46***	0.11	3.86*	—
Tunicates	0.86	7.00**	0.33	—
Teleosts	5.77*	6.90**	1.84	0.59

Although our study showed that chum salmon are primarily planktivorous, like pink and sockeye salmon, we observed another difference in their most important prey. Tunicates (larvacea and salps) were important only in the diets of chum salmon. The IRI for tunicates, especially the larvacean *Oikopleura dioica*, was greater than for any other taxon in chum salmon diets (30.1%). Tunicates were most prevalent in samples from outer coast inlets and outside waters (0–37 km). This finding is not unusual. *Oikopleura* was the dominant prey item in two other studies of the diet of juvenile chum salmon from northern British Columbia: 62% FO in fish 32–106 mm FL from Chatham Sound (Manzer, 1969) and 70–76% FO in fish 105–158 mm FL from Hecate Strait (Healey, 1991).

In addition to interspecific differences in the most important prey, shifts in diet differed among the four salmon species both spatially and temporally. We observed spatial differences in July 1984, when sampling included waters of northern British Columbia, and in August 1984, when sampling was extended to 76 km offshore. Pink, chum, and sockeye salmon consumed fish prey about twice as often offshore as they did inshore, and more often in British Colombia than in Alaska. The more piscivorous coho salmon, however, consumed fish just as frequently inshore as offshore and just as frequently in marine waters of Alaska and British Columbia. Diet varied by season and distance offshore for the highly similar pink,

Table 5

Diet overlap values ($\hat{C}_\lambda$, Morisita's index for prey numbers; Horn, 1966) for inside and outside waters of British Columbia (BC) and Alaska by sampling period and pooled over time. Nearshore = 0–37 km; offshore = >37 km. An asterisk indicates a significant value.

	Diet overlap ($\hat{C}_\lambda$)					
		July 1984		August 1984		
Comparison	Aug 1983	BC	Alaska	Nearshore	Offshore	Pooled over time
Inside inlets						
Pink-chum	0.55		0.87*	0.56		0.66*
Pink-coho	0.89*		0.04	0.29		0.41
Pink-sockeye	—		0.21	0.15		0.37
Chum-coho	0.47		0.11	0.14		0.24
Chum-sockeye	—		0.25	0.85*		0.51
Coho-sockeye	—		0.64*	0.01		0.55
Inside passages						
Pink-chum	0.94*		—	0.91*		0.91*
Pink-coho	0.54		0.11	0.09		0.25
Pink-sockeye	0.85*		0.49	—		0.58
Chum-coho	0.45		—	0.20		0.25
Chum-sockeye	0.74*		—	—		0.73*
Coho-sockeye	0.65*		0.46	—		0.49
Outside waters						
Pink-chum	—	0.44	0.82*	1.00*	0.85*	0.67*
Pink-coho	0.26	0.24	0.10	0.12	0.11	0.20
Pink-sockeye	0.77*	0.85*	0.97*	0.67*	0.79*	0.83*
Chum-coho	—	0.96*	0.10	0.10	0.09	0.32
Chum-sockeye	—	0.39	0.82*	0.53	0.97*	0.68*
Coho-sockeye	0.16	0.20	0.17	0.13	0.09	0.17
All habitats						
Pink-chum	0.95*		0.80*	0.88*		0.91*
Pink-coho	0.43		0.21	0.18		0.38
Pink-sockeye	0.72*		0.79*	0.99*		0.93*
Chum-coho	0.31		0.15	0.25		0.24
Chum-sockeye	0.58		0.73*	0.85*		0.73*
Coho-sockeye	0.62*		0.37	0.18		0.49

chum, and sockeye salmon in the Sea of Okhotsk and the Bering Sea (Andrievskaya, 1968). In our study, temporal patterns based on seasonal (monthly) differences in the FO of fish prey were rare; the diets of pink, chum, or sockeye salmon included fish as frequently in July 1984 (when transects extended only to 37 km) as in August 1984. However, interannual differences were observed: all species, except chum salmon, ate fish more frequently in August 1984 than in August 1983. These observations suggest that increased frequency of fish prey in salmon diets is related more to annual variations in teleost prey abundance than to distance offshore.

Juvenile fishes are often identified as important prey for juvenile salmon, although seldom to the extent that we observed in 1984 in northern southeastern Alaska. Comparison of our results with other studies of juvenile salmon diet in Alaska suggests that, although pink, chum, and sockeye salmon feed principally on planktonic taxa, they readily switch to teleost prey when available. For example, crustaceans were the principal prey of pink, chum, and sockeye salmon in the outside waters of southeastern Alaska in 1982, whereas fish were the principal prey of coho salmon (Jaenicke etal., 1984). In our study in southeastern Alaska in 1983, prey fish made up only half as much biomass as that observed in juvenile sockeye salmon stomachs collected from the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986); in 1984, however, we recorded substantially higher teleost prey biomass than that observed by Hartt and Dell (Table10). Although we found that sockeye salmon diet varied more than that of the other species, increases in the FO of predation on teleosts were consistent among pink, chum, and sockeye salmon.

Some of the interspecific differences in the utilization of fish prey may also be attributed to differences in predator size. The mean size of juvenile coho and chinook salmon was greater than that of pink, chum, and sockeye salmon. Although the importance of size-related variability in prey consumption of juvenile salmon is recognized (e.g. Brodeur, 1991), we considered that a detailed analysis by predator size was beyond the scope of this study.

Increased fish prey in the diets of juvenile salmon in 1984 may reflect higher abundances of larval and juvenile stages of certain prey species compared with the previous year. Unfortunately, most fish prey species found in the salmon stomachs in our study could not be identified. However, we noted opposite trends in the CPUE for two potential teleost prey species from 1983 to 1984: the CPUE of juvenile walleye pollock in our seine catches increased 25-fold whereas that of juvenile herring declined 40-fold. In 1984, juvenile walleye pollock were important in the diet of adult coho salmon (Fisk[3]); the conditions that prolonged offshore feeding by adult coho salmon on these fish in 1984 may also have favored increased piscivory by juveniles.

An increase in available fish prey between years may also correlate with an increase in environmental temperature. The average SST in 1984 ($\bar{x}$=14.5°C) was higher than in 1983 ($\bar{x}$=13.7°C). Increased SST in northern waters may have beneficial effects on the early life history of fish preyed upon by juvenile salmon (Bailey and Incze, 1985). Temperatures in outside waters in 1984 followed a long-term warming trend related to the 1982–83 El Niño event. Temperature increased at depth as well as at the surface, and positive temperature anomalies persisted in northern waters beyond 1983 (Cannon et al., 1985; Royer, 1985). In coastal waters off Oregon and Washington, oceanographic conditions varied greatly owing to the 1982–83 El Niño event and affected prey species composition, but the proportion of fish biomass in juvenile salmon diets generally did not vary for the same months between years (Brodeur and Pearcy, 1990).

Changes in salmonid diet patterns may reflect density-dependent species interactions. Other workers have noted such changes with respect to an increase in the density of pink salmon, typically the most abundant species: 1) the diet of other salmonids became more diverse, particularly in chum salmon; and 2) diet overlap among pink, chum, and sockeye salmon decreased (Birman, 1969; Andrievskaya, 1970; Tadokoro et al., 1996). In the Sea of Okhotsk, diet overlap was lower in the coastal zone, where salmon density was greatest (Andrievskaya, 1970). We did not observe such density effects. We found significant diet overlap even in the four cases out of five where density effects could have been demonstrated among these species (see Jaenicke and Celewycz, 1994). The exception, when chum salmon diet did not overlap significantly with either pink or sockeye salmon diets, occurred during July 1984 in the outside waters of British Columbia.

Density-dependent effects on diet may be reflected in a third dietary attribute, the amount of food consumed. In the eastern coastal zone of the Sea of Okhotsk, for example, 30% of juvenile pink salmon and 66% of juvenile chum salmon sampled with gill nets (time of day not presented) had empty stomachs, a condition not found offshore, where juvenile salmon density was lower (Andrievskaya, 1970). Feeding conditions appeared to be much better for

Table 6

Estimated mean fullness (0=empty, 6=distended), degree of digestion (1=fresh, 4=completely digested), and percentage of empty stomachs for pooled habitats and time periods for juvenile salmon collected in marine waters of southeastern Alaska and northern British Columbia in 1983 and 1984; n = sample size.

Habitat	n	Stomach fullness (0–6)	Degree of digestion (1–4)	Empty stomachs (%)
Pink salmon				
Inside inlet	70	4.0	1.9	0
Inside passage	223	3.9	2.3	0.4
Outer coast inlet	68	3.5	2.7	1.5
Outside (0–37 km)	361	3.0	2.2	3.3
Outside (>37 km)	93	4.0	2.3	0
Chum salmon				
Inside inlet	56	4.2	2.3	0
Inside passage	125	4.7	2.4	0
Outer coast inlet	62	4.6	2.2	0
Outside (0–37 km)	169	2.6	2.7	5.3
Outside (>37 km)	41	3.3	2.4	0
Sockeye salmon				
Inside inlet	24	4.3	2.5	0
Inside passage	58	4.5	3.0	1.7
Outer coast inlet	0	—	—	—
Outside (0–37 km)	227	3.4	2.3	0.9
Outside (>37 km)	52	3.6	2.5	0
Coho salmon				
Inside inlet	159	4.2	2.3	1.3
Inside passage	205	4.4	2.3	0.5
Outer coast inlet	52	4.2	2.5	0
Outside (0–37 km)	115	4.0	2.4	0
Outside (>37 km)	12	4.3	3.0	0

[3] Fisk, G. 1985. Final report 1984 troll logbook program. Alaska Trollers Assoc., 130 Seward St., No. 213, Juneau, AK 99801, 41 p.

Table 7

Neuston and zooplankton organisms (number per 100 m^3) from outside- and inside-water habitats in British Columbia (BC) and Alaska, collected in July 1984.

	Neuston		Zooplankton		
			Outside		
	Outside BC	Combined Alaska	BC	Alaska	Inside Alaska
Number of samples	20	16	3	9	5
Invertebrate eggs	—	—	343.00	1,449,78	304.20
Polychaeta	0.13	0.13	—	—	—
Gastropoda					
Limacina helicina	—	—	124.67	243.67	62.80
Bivalvia	—	—	—	—	26.60
Cephalopoda	0.05	0.13	31.00	—	—
Cladocera	—	—	145.33	524.00	234.20
Calanoida	39.77	114.56	48,672.34	60,074.67	25,956.00
Harpacticoida	0.50	4.31	0	34.33	5.20
Cirripedia	1.90	0.75	187.00	3,203.44	543.40
Mysidacea	—	0.13	0	579.89	—
Gammariidea	0.92	18.17	0	2.22	—
Hyperiidea	126.12	5.21	436.33	566.33	1,142.00
Euphausiacea	8.86	0.17	4,072.70	126.78	164.80
Decapoda	873.11	40.18	363.67	510.33	230.00
Insecta	0.21	0.21	—	—	3.00
Chaetognatha	0.34	5.63	249.33	171.67	42.20
Larvacea	0.15	5.00	62.33	262.78	204.00
Teleosts[1]	1.46	0.79	31.00	6.11	—

[1] Eggs, larvae, and juveniles combined.

salmon in our study (seined during the day); of 2,216 stomachs examined, only 32 (1.4%) were empty. Although we found few empty stomachs, we did find evidence of decreased feeding in the 0–37 km region of outside waters, which includes the region of peak catches of pink and chum salmon (Jaenicke and Celewycz, 1994); fullness was lower for all species, and empty stomachs were most common for pink and chum salmon collected in these outside waters.

Juvenile coho salmon diet rarely showed significant overlap with pink, chum, and sockeye salmon diets. Coho salmon differed in distribution and size from the other three species (Jaenicke and Celewycz, 1994) and were more piscivorous. Curves of cumulative number of taxa (Fig. 3) sloped more steeply for coho salmon than for the other species; this rapid rate of increase in prey types may reflect opportunistic feeding of juvenile coho salmon. Diets are even more diverse among coho salmon individuals than among pink salmon individuals, which consumed a similarly broad array of prey taxa. Less aggregation and lower densities (CPUE) than those for other salmon (Jaenicke and Celewycz, 1994) allow coho salmon to exploit fully all locations within a habitat type. The other three species tended to occur in fewer locations (although they were well represented within habitat types) and tended to be more highly aggregated, increasing the tendency toward more

Table 8

Mean percent similarity index (PSI) values indicating amount of overlap between prey fields and juvenile salmon diet. Stations where prey were collected were included in the analysis for a particular salmon species if at least five stomachs were collected at the station.

	Number of stations	Similarity values	
		Mean	Range
Neuston collection			
Pink	8	10.8	0–24.6
Chum	2	9.3	0–18.5
Sockeye	8	9.1	0–37.8
Coho	2	16.7	0–33.3
Zooplankton collection			
Pink	8	8.0	1.0–22.7
Chum	5	2.2	0.2–6.8
Sockeye	4	9.3	1.0–24.9
Coho	6	6.2	0.7–11.7

Table 9

Prey selection frequencies (Strauss's linear index of food selection (L); Strauss 1979) in juvenile salmon diet for neuston and zooplankton collections, July and August 1984. A positive (pos.) value indicates that a prey was more abundant in the diet than in the environment at a level of ≥0.10. A negative (neg.) value indicates that a prey was less abundant in the diet than in the environment at a level of ≤0.10. A random (ran.) value indicates that a prey was about equally abundant in the diet and in the environment. Absent indicates that a prey item was absent from the diet and from the environment in a particular location. *N* = number of groups tested, where group size was 5 or more of a species.

	Prey selection frequency															
	Pink salmon				Chum salmon				Sockeye salmon				Coho salmon			
Taxon	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent
Neuston																
Polychaetes	0	0	1	7	0	0	0	2	0	0	0	8	0	0	0	2
Pteropods	1	0	2	5	0	0	2	2	0	0	0	8	0	0	0	2
Squid	0	1	0	7	0	0	0	2	0	0	0	8	0	0	0	2
Calanoid copepods	1	1	4	2	0	0	0	2	4	2	1	1	0	0	0	2
Barnacle larvae	0	0	0	8	0	0	0	2	0	1	0	7	0	0	0	2
Gammarid amphipods	0	2	2	4	0	1	0	1	0	1	1	6	0	1	0	1
Hyperiid amphipods	5	1	1	1	1	0	0	1	6	2	0	0	0	1	0	1
Euphausiids	4	1	1	2	0	0	1	1	3	1	1	3	0	0	1	1
Decapod larvae	2	4	1	1	0	2	0	0	2	3	1	2	1	1	0	0
Insects	0	0	1	7	0	0	0	2	0	0	0	8	0	0	0	2
Chaetognaths	0	0	2	6	1	0	0	2	0	0	1	7	0	0	0	2
Salps	0	0	0	8	0	0	0	2	0	0	0	8	0	0	1	1
Larvaceans	1	0	3	4	1	0	0	1	1	0	0	7	1	0	1	0
Teleosts	1	0	5	2	0	0	1	1	0	0	5	3	1	0	0	1
Percent selection	13.5	9.0	20.7	57.4	7.2	10.7	14.3	74.8	14.4	9.0	9.0	67.9	10.8	10.8	10.8	67.7
Plankton																
Cnidaria	0	0	3	5	0	0	2	3	0	0	2	2	0	0	1	5
Polychaetes	0	0	0	8	0	0	1	4	0	0	0	4	0	0	1	5
Pteropods	1	0	1	6	0	0	0	5	0	0	1	3	0	0	1	5
Bivalve larvae	0	0	0	8	0	0	0	5	0	0	0	4	0	1	1	4
Squid	0	0	0	8	0	0	0	5	0	0	1	3	0	0	0	6
Invertebrate eggs	0	2	1	5	0	1	0	4	0	1	0	3	0	0	1	5
Calanoid copepods	0	7	0	1	0	4	0	1	0	4	0	0	0	6	0	0
Barnacle larvae	0	0	2	6	0	0	1	4	0	1	1	2	0	1	1	4
Mysids	0	0	0	8	0	0	0	5	0	0	0	4	0	0	0	6
Hyperiid amphipods	2	0	2	4	2	0	1	2	2	0	1	1	1	0	4	1
Euphausiids	2	0	2	4	1	0	1	3	1	0	1	2	2	0	3	1
Decapod larvae	4	0	1	3	1	0	2	2	2	0	1	1	5	0	1	0
Insects	0	0	0	8	0	0	0	5	0	0	0	4	0	0	2	4
Cladocera	0	0	0	8	0	0	0	5	0	0	1	3	0	0	2	4
Chaetognaths	0	0	2	6	0	0	0	5	0	0	2	2	0	0	1	5
Salps	0	0	1	7	0	0	1	4	0	0	0	4	0	0	1	5
Larvaceans	2	0	1	5	2	0	1	2	0	0	2	2	1	0	3	2
Teleosts	1	0	2	5	1	0	1	3	1	0	3	0	3	0	2	1
Percent selection	8.4	6.3	12.6	73.5	7.7	5.5	12.1	73.7	8.4	8.4	21.0	61.6	11.1	7.4	23.1	58.2

similar diets. Many seine sets caught only coho salmon, whereas catches of the more highly aggregated species often also contained coho salmon. In laboratory experiments, coho salmon smolts in seawater demonstrated agonistic behavior which, if occurring in the wild, would maintain discrete feeding territories and a dispersed population (Paszkowski and Olla, 1985).

Differences in diet, distribution, and size indicate that juvenile coho salmon have a distinct feeding ecology in comparison with these other, more planktivorous, juvenile salmon co-occurring in the southern Gulf of Alaska. In both our study and that of Brodeur and Pearcy (1990), fish were more important in the diets of juvenile coho salmon than in other species. During the second year of our study—when

Table 10

Principal prey of juvenile sockeye salmon in southeastern Alaska and northern British Columbia in 1983 and 1984 and in the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986). Values are percent biomass of total diet. The number of fish sampled is shown in parantheses, followed by fork length ranges (mm).

Prey	Pooled 1967–68 (996) 130–180	Pooled 1983–84 (361) 100–300	August 1983 (55) 130–249	July 1984 (159) 100–209	August 1984 (147) 110–300
Copepods	5.1	0.5	4.6	0.4	0.5
Decapod larvae	—	2.6	8.3	0.8	5.3
Euphausiids	42.0	4.3	39.0	3.4	3.8
Amphipods	1.6	3.7	30.7	2.0	5.1
Pteropods	6.2	—	—	—	—
Larval fish	30.8	87.2	16.7	92.0	83.1

teleost prey increased in all diets—pink, chum, and sockeye salmon readily switched from small zooplankton to larger teleost prey in response to an apparent increase of available larval fish prey. The ability of salmon species to maintain plasticity in their diets may be an adaptation to changing ocean conditions—one that may improve marine survival.

On the basis of our comparisons between the prey composition of juvenile salmonids and the taxa found in neuston and plankton tows, we conclude that these juveniles are selecting a limited subset of available prey. Although other factors besides feeding preferences (e.g. prey patchiness, gear selectivity, differential digestion rates of prey) could lead to low selectivity values, certain taxa do appear to be consumed in high proportions in relation to their abundance. Our results suggest that juvenile salmon are visual predators and select prey on the basis of prey size and visibility and not on local abundance. For example, relatively rare hyperiid amphipods were selected by most salmon, whereas slightly smaller but much more numerous copepods were ignored. As observed by Peterson et al. (1982), this prey selection may be due to the heavy pigmentation and unusual swimming motion of hyperiids in contrast to the light pigmentation and fast swimming motion of copepods.

Although the diets of both chum and coho salmon appear to be more similar to the neuston than the zooplankton catches, a reliance on neustonic fauna, as suggested by Brodeur (1989) for coho salmon off Washington and Oregon, is not conclusively demonstrated because of the small number of comparisons that we were able to make. More detailed field and laboratory studies are required to determine whether juvenile salmon show a reliance on certain prey or an inability to switch to alternate prey when preferred prey resources are depleted. Under these conditions, the availability of the right kinds of prey may have more important implications for the survival of juvenile salmon in coastal waters than the overall production of prey.

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Interspecific comparisons of searobin (*Prionotus* spp.) movements, size structure, and abundance in the temperate western North Atlantic

Richard S. McBride
Marine Field Station, Institute of Marine and Coastal Sciences
Rutgers University
132 Great Bay Blvd., Tuckerton, New Jersey 08087
Present address: Florida Marine Research Institute
100 Eighth Avenue S.E.
St. Petersburg, Florida 33701-5095
E-mail address: mcbride_r@harpo.dep. state.fl.us

Joseph B. O'Gorman
Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Woods Hole, Massachusetts 02543

Kenneth W. Able
Marine Field Station, Institute of Marine and Coastal Sciences
Rutgers University
132 Great Bay Blvd., Tuckerton, New Jersey 08087

Abstract.—Northern searobins, *Prionotus carolinus*, and striped searobins, *P. evolans*, are commonly taken in bottom trawl, pound-net, and hook-and-line fisheries of the temperate, western North Atlantic. Seasonal movements, size structure, and interannual variations in population size of both species were examined with data from three fishery-independent trawl surveys. Geographic distributions of both species overlapped year-round, but on average, northern searobins were found in colder, deeper water than were striped searobins. Northern searobins were found north and east of Cape Cod during the warmest months and northeast of Hudson Canyon during the coldest months, whereas striped searobins were rarely found in these regions during these seasons. Furthermore, northern searobins moved north and nearshore earlier in spring and left these habitats earlier in autumn. Modal size of adult northern searobins was generally between 17 and 21 cm total length, about 5 cm shorter than that of adult striped searobins. Overall, northern searobins were collected more frequently and were more numerous than striped searobins. Because they were smaller and occurred in cooler waters, however, they were not dominant by weight in coastal habitats during autumn. During the past 25–30 years, the annual population size of both species has varied by an order of magnitude, fluctuating without any clear trend. Although seasonally abundant in coastal and continental shelf waters, searobins, because of their small size in relation to other species, are usually discarded and contribute little to landings from the mid-Atlantic states.

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Searobins (family Triglidae) are commonly taken in pound-net and bottom trawl fisheries along the United States east coast but are only occasionally sold as foodfish, lobster bait, or livestock feed (e.g. Goode, 1888; Smith, 1894a). Commercial landings of 100–200 metric tons annually were reported from the mid-Atlantic states during the 1880's (Collins, 1892), 1930's (Marshall, 1946), and 1950's (McHugh, 1977). Millions of searobins are also taken incidentally by hook-and-line recreational anglers (Table 1). Researchers have long recognized the potential for increasing U.S. landings by developing a searobin fishery (Smith, 1894b; Marshall, 1946; Merriman and Warfel, 1948; Perlmutter, 1959–60), but the market potential for searobins is limited by their relatively small size and a false perception that they are poisonous or difficult to handle (Johnson et al., 1987; Murray et al., 1987).

Two searobin species are common in the temperate, western North Atlantic: northern searobin, *Prionotus carolinus* (Linnaeus, 1771), and striped searobin, *P. evolans* (Linnaeus, 1766). They range from Canada to northern Florida (Bigelow and Schroeder, 1953; Gilmore, 1977; Scott and Scott, 1988; Russell et al., 1992) but are most common year-round on the continental shelf from Cape Cod to Cape Hatteras (Nichols and Breder, 1926; Hildebrand and Schroeder, 1928; Edwards et al., 1962). Life history information is provided in Marshall (1946), Wong (1968), McEachran and Davis (1970), Richards et al.

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(1979), Yuschak and Lund (1984), Yuschak (1985), Keirans et al. (1986), and McBride and Able (1994).

This study describes and compares the seasonal movements, size structure, and interannual variations in population size of northern and striped searobins in the Mid-Atlantic Bight. No previous study has synthesized searobin data over such a large geographic scale. The present and potential roles of searobins in fisheries of the temperate western North Atlantic are also discussed.

Table 1

Estimated numbers of searobins (all triglid species combined) caught by marine recreational anglers from 1979 to 1991 in the Mid-Atlantic, as well as in all subregions of the U.S. east coast combined: Gulf of Maine, Mid-Atlantic, South Atlantic, and Gulf of Mexico. Data prior to 1979 are not available.

	Numbers (in millions)		
Year	Mid-Atlantic	U.S. east coast	Source
1979	3.548	5.145	Holliday, 1984
1980	7.102	7.957	Holliday, 1984
1981	1.624	2.613	NMFS, 1985a
1982	2.795	5.074	NMFS, 1985a
1983	8.750	10.058	NMFS, 1985b
1984	6.189	6.752	NMFS, 1985b
1985	3.562	4.361	NMFS, 1986
1986	10.908	11.858	NMFS, 1987
1987	4.824	5.071	Essig et al., 1991
1988	5.182	5,899	Essig et al., 1991
1989	2.631	2.947	Essig et al., 1991
1990	4.896	5.518	Van Voorhees, et al.,1992
1991	7.254	7.799	Van Voorhees, et al.,1992
Mean (per yr)	5.328	6.235	
Total	69.265	81.052	

Materials and methods

Data were derived from three fishery-independent bottom trawl surveys (Table 2). One survey, conducted by the National Marine Fisheries Service, covered the entire Mid-Atlantic Bight (i.e. the coastal region from Cape Cod to Cape Hatteras), as well as Georges Bank and the Gulf of Maine (Fig. 1). Data from two regional surveys were also examined: one at the northern extent of the Mid-Atlantic Bight near Cape Cod, the other within a central portion of the Mid-Atlantic Bight offshore of New Jersey. In each survey a stratified, random design was used for allocating trawl tows. Strata were established by depth categories and other physiographic boundaries. Numbers of tows within each stratum were proportional to stratum area; within each stratum, tow locations were randomly assigned. Fishes were counted and weighed; measurements were reported to the nearest centimeter total length (TL). In preliminary analyses geographic and length-distribution data were plotted for all years available, but herein only data from selected cruises (1991–92) are graphed. Preliminary calculations of abundance showed that

Table 2

Sources and details of trawl data examined for this study. Data for the period 1982–91 were the focus of most analyses. Data regarding distribution and size structure for the years 1991–92 were plotted (Figs. 2–7) as representative years.

Data source	Trawl headrope (m) (mesh [mm])	Tow time (min)	Season	Month	Sampling depth (m)	Years
Throughout the Mid-Atlantic Bight						
NEFSC, NMFS[1]	18.3–19.8	30	Spring	Mar–May	9–366	1968–95
	(12.7)	30	Summer	Jun–Aug	9–200	1963–65,69,77–81
		30	Autumn	Sep–Nov	9–366	1963–95
		30	Winter	Dec–Feb	9–200	1964–6,78,81,91–2
Offshore of Massachusetts and New Jersey						
MDMF[2]	11.9	20	Spring	May	9–55	1978–95
	(12.7)	20	Autumn	Sep	9–55	1978–95
NJBMF[3]	24.4	20[4]	5–6/year	Jan–Dec	6–27	1988–92
	(6.3)					

[1] Northeast Fisheries Science Center, National Marine Fisheries Service.
[2] Massachusetts Division of Marine Fisheries.
[3] New Jersey Bureau of Marine Fisheries.
[4] Tows in 1988 were for 30 minutes.

fish numbers and weight had similar trends (McBride, 1994); therefore only weight indices are reported here. Some descriptive statistics were also based on subsets of data (1982–91), as noted below. Statistical significance was evaluated at $P<0.05$. The above comments pertain to all data examined, and comments below outline procedures specific to each sampling program.

NMFS sampling

Survey data from the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC), were examined. The survey area was divided into 76 strata from Cape Fear, North Carolina, to Cape Sable, Canada, in waters 9–366 m deep. Spring and autumn cruises sampled a total of about 350 stations during a 6–8 week period, whereas summer and winter cruises sampled about half as many stations (Table 2). The primary gear used was a no. 36 Yankee trawl. In spring, summer, and autumn cruises a roller-rigged footrope was used; however, in winter cruises a cookie sweep and ground cable designed to target flatfish were used. Latitude, longitude, and depth were recorded at the start of each tow. Bottom temperature was usually recorded by using an XBT cast or a CTD probe. See Grosslein (1969, 1976), Azarovitz (1981), and Despres-Patanjo et al. (1988) for further sampling details.

Exploratory data analyses considered all 76 strata, but interannual comparisons of abundance considered only latitudinal strata within the Mid-Atlantic Bight because both species were uncommon or absent in the Gulf of Maine and on Georges Bank and because sampling south of Cape Hatteras was not broad in coverage or consistent between years. Because the distribution of both species varied seasonally, largely as an onshore–offshore pattern, different depth strata sets were used for calculating spring and autumn abundances; the autumn strata selected were generally <27 m and the spring strata were >27 m deep. Because the purpose here was to compare interspecific abundances, the final selection of strata included the broadest possible latitudinal range within the Mid-Atlantic Bight where both species occurred.

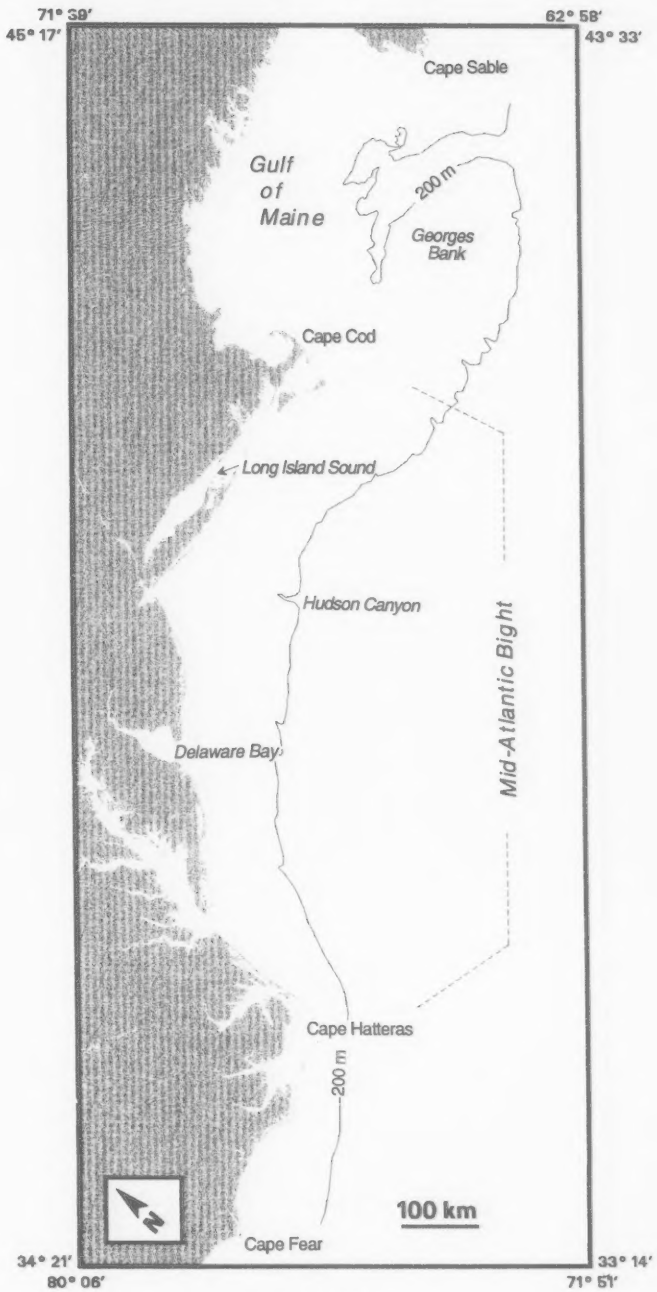

Figure 1

Study area of the U.S. east coast, with some landmarks identified in the text (additional landmarks are depicted in Fig. 3). The Mid-Atlantic Bight is defined as the coastal region between Cape Cod and Cape Hatteras. Sampling strata for the Mid-Atlantic Bight survey (NEFSC, NMFS, Table 2) extended in total from Cape Fear to Cape Sable. Sampling regions for the Massachusetts and New Jersey surveys (Mass. Div. Mar. Fisheries and New Jersey Bureau of Mar. Fisheries; Table 2) are depicted in Figures 3 and 4.

The autumn strata selected were NMFS inshore strata identification numbers 01–61, and the spring strata were NMFS offshore strata 01–12, 25, and 61–72. The summer and winter seasons were not sampled consistently enough to be included in these comparisons of abundance. Abundance of each species was estimated as a stratified mean weight per tow with the methods of Finney (1941) and Pennington (1983). These values are log-transformed (ln[x+1]) means, weighted by stratum area.

Regional sampling

The Massachusetts Division of Marine Fisheries (MDMF) sampled 23 strata along the Massachusetts shoreline (<55 m). Approximately 80–90 stations were sampled in May and again in September (Table 2) with a 3/4 North Atlantic type-2 seam trawl at random locations, except where precluded by untowable bottom and extensive fixed commercial gear (Howe, 1989). Abundance indices were calculated in the same manner as those calculated for the sampling by NMFS (see above). Strata were selected to encompass an area where both species occurred in each season (MDMF strata no. 10–19 for spring; 11–12 for autumn).

The New Jersey Bureau of Marine Fisheries (NJBMF) sampled 15 strata along the New Jersey coast (<27 m). Cruises occurred every 6–10 weeks during 1988–92 (Table 2). Each cruise sampled 25–39 stations during a 1–4 week period using a 3-in-1 trawl at random locations (Byrne, 1989). Mean weight per tow (ln[x+1]) was calculated without weighting for strata areas, and tows from all strata were used because both species occurred throughout the NJBMF sampling area during most of the year.

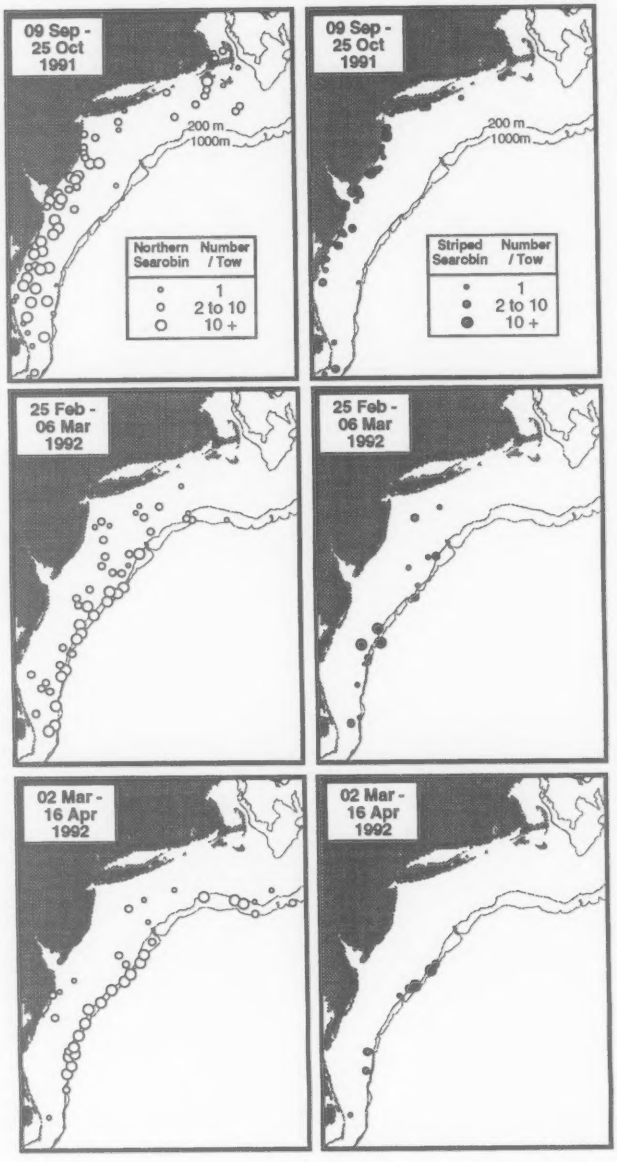

Figure 2

Geographic distribution of northern searobins (open symbols, left column) and striped searobins (filled symbols, right column) in the Mid-Atlantic Bight during autumn, 1991 (top), winter, 1992 (middle), and spring, 1992 (bottom) based on Northeast Fish. Sci. Center, NMFS, resource surveys (Table 2). Much of the Gulf of Maine and Georges Bank are not depicted here because sampling there collected only a single northern searobin (at a station immediately north of Cape Ann; see Fig. 3 for landmark reference).

Results and discussion

Movements

Northern searobins, but not striped searobins, moved seasonally between the Mid-Atlantic Bight and the Gulf of Maine, and they used habitats on Georges Bank (Figs. 2 and 3). Striped searobins occurred rarely north or east of Cape Cod in any year, but northern searobins, although not common there, oc-

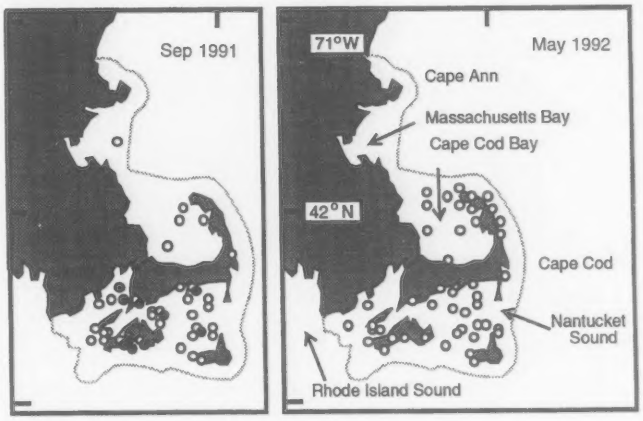

Figure 3

Geographic distribution of northern searobins (open symbols) and striped searobins (filled symbols) during two consecutive sampling seasons for the Massachusetts coastal survey (Table 2). The dotted line represents the offshore limit of sampling (55 m).

curred annually on parts of Georges Bank and in the southern portion of the Gulf of Maine during summer and autumn. In general, both species were broadly distributed within the central Mid-Atlantic Bight but moved southward during winter and spring (Figs. 2 and 4). Striped searobins moved well south and west of Hudson Canyon, which appears as an approximate northern limit for striped searobins during the overwintering season, whereas northern searobins had a broader latitudinal distribution in the Mid-Atlantic Bight while overwintering (see also McBride and Able, 1994). These data suggest that by spring large striped searobins moved either farther offshore into continental slope waters (>200 m) or migrated south of the zoogeographic boundary represented by Cape Hatteras (i.e. between the Mid-Atlantic and the South Atlantic Bight) because sizes > 25 cm TL are uncommon during spring cruises (Fig. 5). We cannot prove this hypothesis, however, because these southern and offshore regions were not well sampled during the overwintering season (see Table 2 for sampling area limits).

Both searobin species migrated seasonally in an onshore–offshore direction as well as in a north–south direction (Fig. 2). Northern searobins were, however, consistently found in significantly deeper waters than were striped searobins during both spring (78.3 m ± 5.27 vs. 60.4 m ± 9.30; mean depth ± 95% confidence limits [CL]) and autumn (30.7 m ± 1.73 vs. 20.0 m ± 1.44) during 1982–91. Northern searobins were also found in significantly colder bottom temperatures than were striped searobins in spring (9.2 ± 0.3°C vs. 11.8 ± 0.56°C; mean ± 95% CL) and autumn (17.6 ± 0.40°C vs. 19.6 ± 0.40°C), although both species were collected in a wide range of temperatures (4–28°C) during 1982–91. These results support McBride and Able's (1994) postulation that temperature is the principal factor producing distinctive geographic distributions for each species. Other western North Atlantic searobins (*Prionotus* and *Bellator* species) that are distributed in subtropical and tropical waters reside within species-specific depth regions but show little tendency to migrate seasonally (Lewis and Yerger, 1976; Ross, 1977; Floyd, 1980; Hoff, 1992). South of Cape Hatteras, where temperatures fluctuate less between seasons than in the Mid-Atlantic Bight, even northern searobins show little tendency to migrate seasonally (Floyd, 1980).

Size structure

Modal size of northern searobins was consistent between seasons (17–21 cm TL), but striped searobins were both larger and more variable in size (18–28 cm TL; Fig. 5). The larger size of *P. evolans* is largely accounted for by its faster growth rate and greater maximum age (Richards et al., 1979). An earlier analysis of NMFS survey data has reported northern searobins as large as 34 cm and striped searobins as large as 41 cm (Wilk et al., 1978). The maxima observed in our study were 5–7 cm larger, but these

are most likely the result of much larger sample sizes (total for combined species was 1,314 fish measured in 1974–75 [Wilk et al., 1978] vs. 69,072 in 1982–91[our study]). Briggs (1977) reported a single record of a striped searobin measuring 485 mm TL, which equaled the size of our largest striped searobin. Floyd (1980) reported the largest northern searobin as 26 cm TL (n=1795) and the largest striped searobin as 35 cm TL (n=47) based on trawl collections south of Cape Hatteras. These findings support Ginsburg's (1950) observation that searobin size increases with higher latitudes.

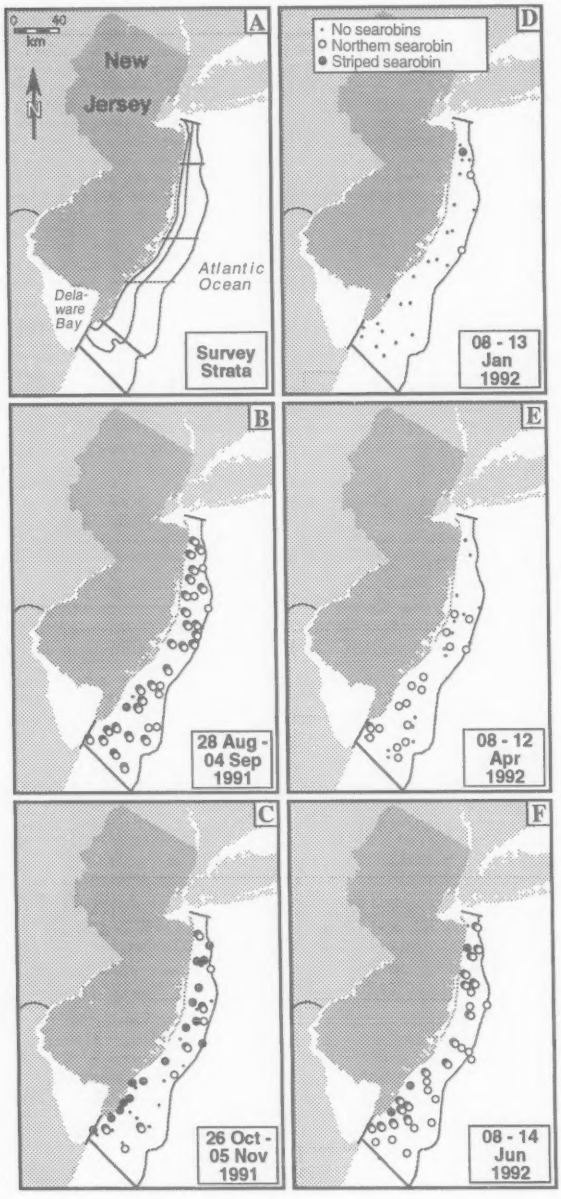

Figure 4

Seasonal distributions of northern searobins (open symbols) and striped searobins (filled symbols) during five consecutive cruises for the New Jersey coastal survey (Table 2).

Young-of-the-year (YOY) of both species were evident in all surveys (Figs. 5–7), particularly during autumn months, when a size of 15 cm TL was used to separate YOY from older year classes (Richards et al., 1979; McBride and Able, 1994). Collections from Massachusett waters did not indicate overwintering by YOY searobins near Cape Cod, a finding similar to that reported by Richards et al. (1979). In New Jersey nearshore waters, YOY northern searobins were evident in April, suggesting that they had migrated back inshore in this region much sooner than had been observed farther north.

Abundance

Northern searobins were more abundant than striped searobins by numbers and frequency of occurrence. A total of 66,064 northern searobins were collected in 1,125 tows, whereas only 3,008 striped searobins were collected in 366 tows out of a total of 7,369 NMFS tows during spring and autumn, 1982–91. Both species were caught together in 202 of these 7,369 tows. In Massachusetts waters, northern searobins were also more numerous than striped searobins in spring (88,565 vs. 75 fish) and autumn (10,966 vs. 374 fish) during 1982–91. And in New Jersey waters, northern searobins were more numerous than striped searobins (35,471 vs. 5,258 fish) in 700 tows during 1989–92. Northern searobin aggregate weight was not, however, always heavier in coastal waters during autumn (Figs. 8 and 9) because striped searobins weigh more on average and because striped searobins occupy inshore habitats more frequently in the warmest season. In proximity to New Jersey, northern searobins appear to migrate inshore earlier, peak in abundance earlier, and move offshore earlier than striped searobins, a behavior consistent with their postulated temperature preference.

The Mid-Atlantic Bight (NMFS) time series of stratified mean weight per tow was

highly variable (for northern searobins, CV=48 in spring and 49 in autumn; for striped searobins, CV= 68 in spring and 101 in autumn; Fig. 8) but showed no clear trend over time. There was one notable period of decline for northern searobins during spring surveys throughout the 1970's, but there was also a modest rebound in abundance during the 1980's. The low values in the early 1990's were similar to values measured in the late 1960's. The abundance of northern searobins during autumn cruises suggested no trend but was punctuated with sporadic peaks. Striped searobins also appeared to be more abundant during the 1970's than in the 1960's or 1990's, according to spring indices. The autumn time series for striped searobins declined overall, until the last year (1995), which showed a sudden increase. Abundance was compared between species to establish if each species' population size followed similar seasonal and interannual trends. Correlation analyses detected a significant relation between northern and striped searobin annual indices measured in the spring survey (Spearman rank correlation, r_s=0.47, P=0.01, n=28), but the correlation between species abundance in the autumn surveys was not significant (r_s=0.006, P=0.97, n=24). The spring and autumn indices for a given year were not significantly correlated for northern searobins (r_s=0.14, P=0.51, n=24) but were significantly correlated for striped searobins (r_s=0.65, P=0.0006, n=24). These latter results suggested that the selected spring and autumn strata measured similar trends of abundance for striped searobins but not for northern searobins.

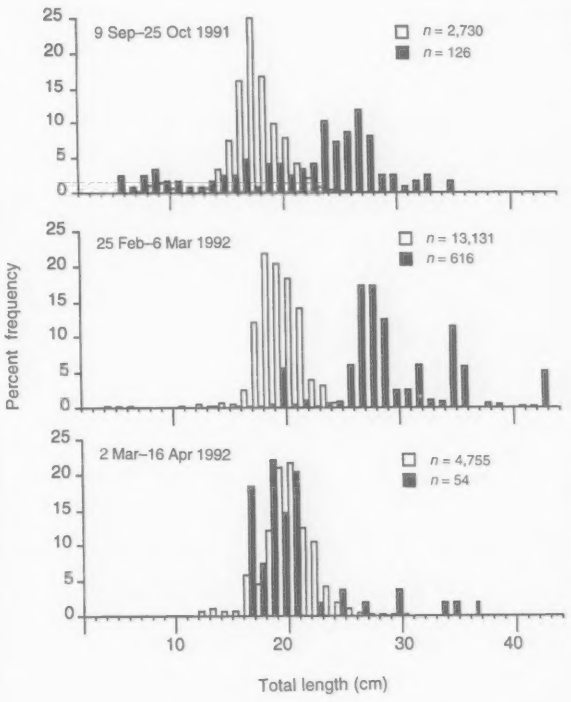

Figure 5

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) in the Mid-Atlantic Bight during autumn, winter, and spring, 1991–2, based on the Northeast Fish. Sci. Center, Natl. Mar. Fish. Serv. resource surveys (Table 2). Sampling periods are the same as those shown in Figure 2. n=number of fish.

Earlier estimates of searobin population size also noted considerable yearly variations in abundance. Clark and Brown (1977) reported a dramatic 97% decline in abundance (by weight) of searobins in the southern Mid-Atlantic region (also depicted in Grosslein [1976]) based on the same database during the period 1967–74. But they also reported a 143% increase in abundance of searobins in the southern New England region. It is difficult to compare their results with our Figure 8 because they grouped northern and striped searobins together. They also used autumn collections from offshore strata sets, but our autecological analyses revealed these strata as only marginally appropriate, at least for striped searobins that are still inshore during autumn. Their analysis of abundance reviewed years during which fairly rapid change was occurring for both searobins and the groundfish assemblage in general, but our analyses demonstrate that searobin abundance has fluctuated up and down since the early 1970's.

Northern searobin annual abundance in the Massachusetts coastal survey has also shown large long-term variations (Fig. 8). Modest increases for northern searobin abundance in the early 1990's barely offset dramatic declines during the 1980's. In contrast, there was no trend in abundance of striped searobins during this 20-year period. These indices could be biased with respect to interannual variations in coastal temperatures because Murawski (1993) demonstrated that the latitudinal range of northern searobins varied between years with respect to sea-temperature anomalies. Thus, one might expect that searobins are more abundant in coastal Massachusetts waters during warmer years. Such does not appear to be the case, however, because

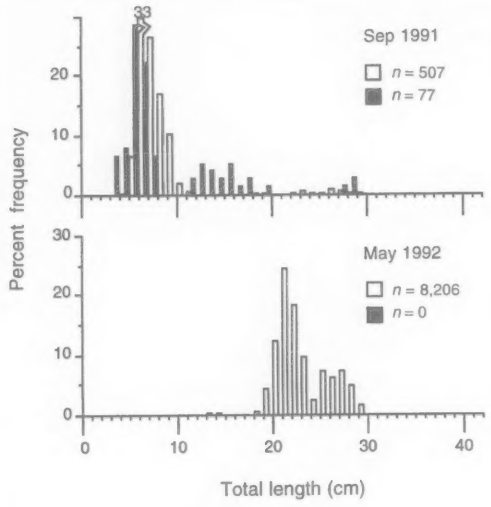

Figure 6

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) for the Massachusetts coastal survey. Sampling periods are the same as those shown in Figure 3. *n*=number of fish.

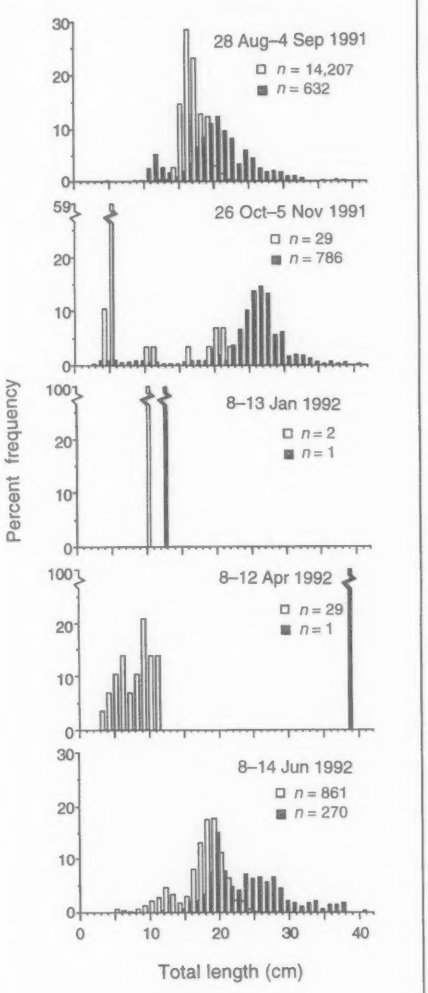

Figure 7

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) during five consecutive cruises for the New Jersey coastal survey (Table 2). Sampling periods are the same as those shown in Figure 4. *n*=number of fish.

Murawski reported that after an anomalously warm period in the 1970's (when northern searobin abundance did increase) temperatures in the 1980's fluctuated without a trend (but northern searobin abundance declined dramatically; see Fig. 8).

The indices of stratified mean weight per tow between the Mid-Atlantic Bight (NMFS) and the Massachusetts (MDMF) surveys were compared to examine how robust these measures of abundance were. Correlation analyses revealed a significant relation between northern searobin abundance in spring (r_s=0.51, P=0.032, n=18) between the two surveys, but autumn abundances in similar years were negatively correlated between the two surveys (r_s=-0.60; P=0.008, n=18). There was a significant relation between these surveys for striped searobin abundance in spring (r_s=0.51, P=0.029, n=18) but not for autumn (r_s=0.077, P=0.76, n=18). These significant, positive relations between the two surveys support our use of spring but not autumn indices for examining northern and striped searobin population trends.

Implications for fishery ecology

Northern and striped searobins belong to a "warm-temperate" group (Musick et al., 1989), an assemblage that migrates onshore and north as temperatures increase, offshore and south as temperatures decline. Our descriptive analysis supports this characterization of both species but reveals interspecific differences in the timing and extent of seasonal movements, as well as in size and abundance. Selection of sampling strata for calculating abundance indices was constrained by our goal to compare the ecology of both species. Nevertheless, indices from spring cruises in the Mid-Atlantic Bight and along the Massachusetts coast were significantly and positively

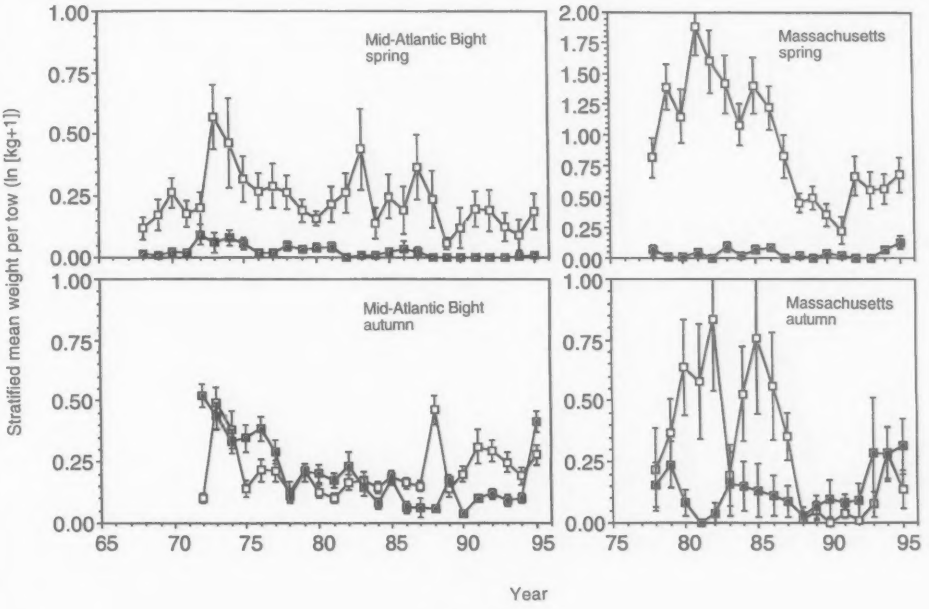

Figure 8

Annual biomass indices for northern searobins (open symbols) and striped searobins (filled symbols). Mid-Atlantic Bight indices (left) are based on sampling by Northeast Fish. Sci. Center, NMFS, resource surveys (Table 2). Massachusetts indices (right) are based on the Massachusetts (Mass. Div. Mar. Fisheries [MDMF]) coastal surveys (note the scale of the ordinate is doubled for MDMF Spring). All values are log-transformed and plotted with ±1 standard error bar. See text for details of strata selection and statistical calculations (e.g. spring and autumn strata are different).

correlated, so that they were especially useful in evaluating population trends. On the other hand, the inshore strata selected for autumn cruises in the Mid-Atlantic Bight were adequate for sampling striped searobins but were too shallow for northern searobins because the latter occupied a mean depth of 31 m during that season.

Searobins are not important fishery species in the United States but are components of bycatch in commercial and sport fisheries; their population sizes could be affected by fishing or other factors. However, their population size varied without a specific directional trend during three decades. The long-term trend of annual biomass indices for searobins is similar to other demersal finfish such as white hake (*Urophycis*

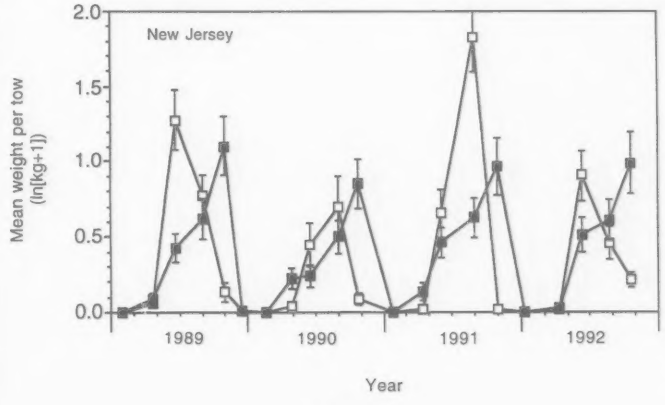

Figure 9

Seasonal abundance of northern searobins (open symbols) and striped searobins (filled symbols) based on all cruises (1989–92) for the New Jersey coastal survey (Table 2). Abundance is depicted as mean weight (± 1 standard error) of all tows per cruise. Cruises typically lasted one week, and a mean date value was used to plot each cruise.

tenuis), cusk (*Brosme brosme*), scup (*Stenotomus chrysops*), and ocean pout (*Macrozoarces americanus*) (U.S. Dep. Commerce, 1993). In contrast, population declines have been characteristic of traditional groundfish and flounder species, and aggregate biomass of principal pelagic species, skates, and spiny dogfish have increased in the western North Atlantic (U.S. Dep. Commerce, 1993).

Fishery landings, value, and catch rates for mid-Atlantic states have all declined over the past several decades (McHugh and Conover, 1986), and underused species such as searobins have limited potential to counter these trends. Our survey results, for New Jersey in particular, show that searobins are seasonally abundant in areas amenable to inshore commercial and recreational fisheries during summer and autumn. Trawlers can also find large aggregations offshore during winter and spring. Searobins are also a large proportion of pound-net landings during summer, although this fishing method is now reduced in comparison with historical levels (McHugh and Conover, 1986). Striped searobins may be a more marketable species because they are larger on average. Efforts to expand the marketability of searobins, such as has occurred recently by selling them live in restaurants (Lynch[1]), may lead to increased total landings and a more diverse fishery resource for the mid-Atlantic region.

Acknowledgments

We thank the crew and scientists aboard the RV's *Albatross IV*, *ARGO Maine, Delaware II, Gloria Michelle*, and the FV *Amy-Diane* as well as T. Azarovitz (NEFSC, NMFS), P. D. Byrne (NJBMF), and A. Howe (MDMF) who provided data for analysis. R. Cowen, M. Fahay, J. P. Grassle, R. Loveland, and C. L. Smith made helpful comments in discussions and on earlier drafts. J. Bexley produced Figure 1. This study, part of a doctoral dissertation (R.S.M.), was supported by the Institute of Marine and Coastal Sciences (IMCS-Rutgers), Rutgers University Marine Field Station, Manasquan Marlin and Tuna Club, NOAA National Undersea Research Program for the New York Bight, NOAA Sea Grant Program, and the Fisheries and Aquaculture TEX Center (Rutgers). Final revisions were made while the senior author was at the Florida Marine Research Institute, Florida Department of Environmental Protection.

[1] Lynch, T. R. 1993. Rhode Island Department of Environmental Management, 150 Fowler Street, Wickford, Rhode Island 02852. Personal commun.

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Abundance, growth, and mortality of young-of-the-year pinfish, *Lagodon rhomboides*, in three estuaries along the gulf coast of Florida

Gary A. Nelson

Florida Marine Research Institute
Department of Environmental Protection
100 Eighth Avenue SE
St. Petersburg, Florida 33701-5095

E-mail address: nelson_ga@sellers.dep.state.fl.us

Abstract.—Fixed-station and random-sampling data from 1989–94 were used to examine spatial and temporal patterns in abundance and size structure of young-of-the-year (YOY) pinfish, *Lagodon rhomboides*, in three Florida estuaries. Young-of-the-year pinfish first appeared at shallow-water (<1.4 m) seine stations in November in Choctawhatchee Bay (Florida Panhandle), and in December in Tampa Bay and Charlotte Harbor, both along the southwest Florida peninsula. Pinfish were caught at deep-water (>1.6 m) trawl stations within one month after their initial appearance at shallow-water (<1.4 m) sites in Choctawhatchee and Tampa bays. However, YOY were absent in the deep water of Charlotte Harbor until 1–3 months after their first appearance in shallow water. Most YOY pinfish were caught in waters <3.5 m. Young-of-the-year pinfish in shallow-water areas were associated with bottom vegetation, mostly seagrasses, in all bays. Annual variation in YOY abundance was correlated with variations in adult abundance in Tampa Bay and with temperature in Charlotte Harbor. Instantaneous growth rates were rapid (0.10 to 0.26/month) and were similar to published rates for other Florida and gulf coast populations. Similar rates of total instantaneous mortality (0.021 to 0.023/day) were estimated for all bay populations.

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Fishery Bulletin 96:315–328 (1998).

Young-of-the-year pinfish, *Lagodon rhomboides*, play important ecological roles in the northeastern Gulf of Mexico as prey for fish (Carr and Adams, 1973; Seaman and Collins, 1983) and as predators on a range of invertebrates, often to a degree where entire assemblages of macrobenthic fauna are affected (Young et al., 1976; Young and Young, 1977; Nelson, 1978). In addition, YOY pinfish are an important link between primary and secondary production because they consume seagrasses (Stoner, 1982; Weinstein et al., 1982; Montgomery and Targett, 1992).

Despite the ecological importance of pinfish, their population dynamics have been inadequately examined. It is unknown if seasonal changes in abundance or movements occur throughout entire estuaries, if growth rates are similar among populations, or if abundances fluctuate annually because past studies have had limited spatial coverage (usually 1–4 seagrass sites were sampled in waters <2 m) and short sampling durations (<2 yr)(Reid, 1954; Caldwell, 1957; Hellier, 1962; Hoese and Jones, 1963; Cameron, 1969; Hansen, 1970; Stoner, 1983). In addition, factors that may influence year-class strength have not been examined, and mortality rates have not been estimated.

In this study, I use two to six years of data to document seasonal changes in abundance, distribution, and movements within shallow- and deepwater areas to identify factors that may influence spatial and annual abundance and to estimate and compare growth and mortality rates among three estuarine populations of YOY pinfish along the gulf coast of Florida, USA.

Methods

Young-of-the-year pinfish were studied in 1) Choctawhatchee Bay and Santa Rosa Sound (surface area: ca. 450 km^2), located in the western Florida Panhandle, 2) Tampa Bay (ca. 886 km^2), and 3) Charlotte Harbor (ca. 575 km^2), the latter two located on the gulf side of the Florida peninsula (Fig. 1). All three bay systems are characterized by average depths of <5 m, salinities of 0–36 ppt, freshwater inflow from rivers, and expanses of bottom vegetation, primarily seagrasses (*Halodule wrightii* and *Thalassia testudinum*), in shallow areas. Seasonal mean water temperatures range from 10 to 29°C in Choctawhatchee Bay and Santa Rosa

Sound, from 15 to 30°C in Tampa Bay, and from 18 to 32°C in Charlotte Harbor.

Pinfish were sampled monthly from 1989 to 1994 at fixed seine and trawl stations. Fixed stations were approximately evenly distributed throughout shallow- and deepwater areas and included sites in major rivers in Tampa Bay and Charlotte Harbor. Monthly sampling began in 1992 in Choctawhatchee Bay, in 1989 in Tampa Bay, and in 1991 in Charlotte Harbor. Samples were collected with a 21.3-m × 1.8-m, 3.2-mm stretched-mesh seine, or a 6.1-m, 38-mm stretched-mesh otter trawl containing a 3.2-mm stretched-mesh codend liner. At beach stations, seines were set adjacent to the shoreline and hauled onshore; at offshore stations (<1.4 m), seines were set in open-water habitats away from the shoreline and retrieved offshore. In rivers, seines were set from the shoreline in a semicircular pattern from a boat. In deep water (>1.6 m), trawls were towed 1 knot for 5 min at river sites and for 10 min at bay sites. Three hauls or tows were made at each fixed station during daylight hours. Sampling occurred during the first two weeks of each month.

Pinfish were also sampled in spring (March to June) at randomly selected sites to provide more accurate estimates of YOY abundance. To coordinate sampling logistics, each bay was subdivided into 5–6 arbitrarily lettered, permanent zones (bay: zones A–E; rivers: zone F). All bay zones encompassed about equal area. Within each zone, 1' latitude × 1' longitude microgrids, representing the sites to be sampled, were randomly selected within randomly selected 1° latitude × 1° longitude grids. Sampling entailed randomly selecting a zone and then sequentially sampling all sites within each zone. At each site, three hauls were made with the same gears and deployment techniques used at fixed stations. Random sampling began in Choctawhatchee Bay in 1993 and in Tampa Bay and Charlotte Harbor in 1989 and occurred over eight, twelve, and ten weeks, respectively.

For all hauls, total numbers of pinfishes were counted, standard lengths were measured (±1 mm) for 20 randomly selected individuals per sample, and all fish were released. When large numbers of individuals (>1,000) were captured, the total number was estimated by fractional expansion of subsampled portions of the total catch split with a modified Motoda splitter (Motoda, 1959). Salinity (ppt), temperature (°C), depth (m), and bottom types were also recorded at all sites. Dominant vegetation types were recorded at seine sites only.

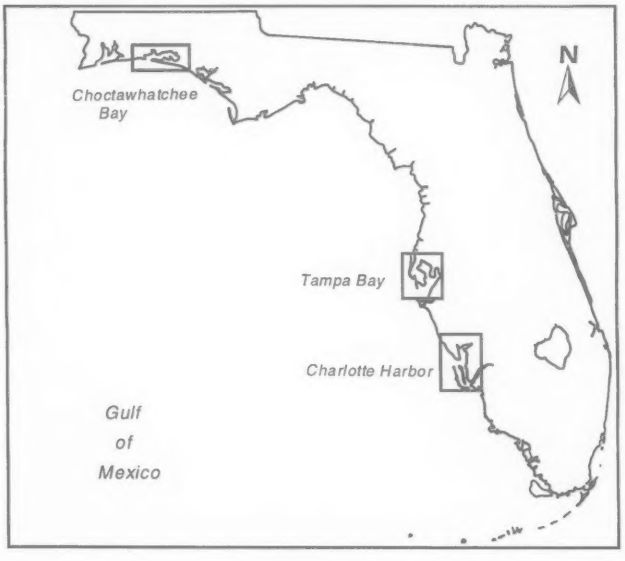

Figure 1

Map of Florida showing the locations of Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor.

Seasonal changes in YOY abundance and size structure

To examine seasonal changes in YOY abundance in shallow- and deepwater areas, comparable monthly mean number of individuals per 100 m^2 were calculated from fixed station data by year. I separated YOY data used in all analyses from data on older individuals by using maximum size limits selected from monthly length-frequency plots. Monthly length frequencies based on proportions of fish found in each length class were combined over years to describe within-year trends rather than year-to-year variability. Length maximum size limits used for Choctawhatchee Bay data were in agreement with the maximum lengths of scale-aged YOY pinfish from Pensacola Bay (Hansen, 1970).

Depth distribution

To determine whether YOY were restricted to depth ranges during the period surrounding peak abundance, the cumulative frequency distributions of trawl and YOY pinfish depth occurrences were compared by using the Kolmogorov-Smirnov test (Perry and Smith, 1994). The cumulative frequency distributions for YOY pinfish were constructed by weighting depth at each random site by the number of YOY pinfish captured at that site. Only spring data from the first

trawl made at each random site were used to ensure independence of observations. Data from 1989–94 were combined to examine within-year trends rather than year-to-year variability.

Factors influencing spatial YOY abundance

I examined variation in YOY pinfish abundance in shallow-water areas for year, deployment technique, month, zone, sediment type (mud or sand), absence or presence of bottom vegetation (mostly seagrasses), temperature, and salinity effects by bay. Spring catch data (transformed by using $\ln(x+1)$ prior to analysis) from the first seine haul at each randomly selected site were analyzed with general linear models (GLM; Hilborn and Walters, 1992) and PROC GLM (SAS Institute, 1988). Year, month, deployment technique, zone, sediment type, and bottom vegetation were treated as main effects, and temperature and salinity (transformed by using $\ln(x+1)$ prior to analysis) as covariates. All first-order interactions of the main effects were also tested. Any variable or first order interaction not significant at $\alpha = 0.05$ with type-III (partial) sum of squares was dropped from the initial GLM model and the analysis was repeated. In addition, least squares means and their 95% confidence intervals (Searle et al., 1980; SAS Institute, 1988) from the GLM's were back-transformed (Sokal and Rohlf, 1981) to examine significant abundance and main effect relationships.

Initial analyses revealed that the only significant first-order interactions were related to the random selection of zones for sampling. Because these interactions were not considered relevant to this study, they were absorbed in the error term, and the main effects and covariates were retested.

Factors influencing YOY annual abundance

To determine if annual variations in YOY abundance were correlated with variations in temperature, I compared annual relative abundance indices (least squares means for the effect of year) to monthly means of sea-surface temperature before and during the first appearance of YOY pinfish, using Pearson product moment correlation (Sokal and Rohlf, 1981; Tyler, 1992). Temperature data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) oceanographic monthly summary series.

I also used Pearson product moment correlation to determine if annual variations in YOY relative abundance were correlated with variations in adult abundance. Adult (>80 mm SL) pinfish abundance indices were derived from data collected in the Marine Recreational Fisheries Statistics Survey (MRFSS on Florida's west coast in 1988–93)(U.S. Dep. Commer., 1990; 1992). The GLM approach was used only to derive annual least-squares mean catch-per-intercept estimates (relative abundance) by adjusting the total number of fish caught per intercept for the classification variables of two-month sampling wave, fishing mode (party or charter boat, private or rental boat, or shore-based fishing boat), area fished, counties where interviews were conducted, and for the covariates of number of anglers per intercept and hours fished by anglers. All variables were significant contributors to the overall variation in catch rates in Tampa Bay (model: $F_{[28,3853]}=11.55, P<0.001, r^2=0.08$), but only year, sampling wave, county, and hours fished by anglers were significant for Charlotte Harbor (Model: $F_{[20,1060]}=5.74, P<0.001, r^2=0.10$).

Growth

I examined annual growth of YOY by estimating instantaneous growth rates (G) using mean lengths for each bay and year. Growth was estimated with the following model:

$$\ln L_t = \ln L_0 + G \times t,$$

where G = the instantaneous growth rate (per month);
L_t = monthly mean length (mm);
L_0 = the theoretical length at which pinfishes recruit to each bay; and
t = time in months (Ricker, 1975; DeAngelis et al., 1980).

Mortality

Daily instantaneous total mortality rates were estimated for each bay population of pinfish by means of the relationship

$$Z = \frac{-\ln\left(\frac{N_{t+1}}{N_t}\right)}{30},$$

where Z = the daily instantaneous total mortality; and
N = the index of relative abundance at months t and $t+1$ (Ricker, 1975).

Monthly indices of relative abundance from fixed seine stations were used in the equation. Although immigration and emigration in the shallow-water areas can bias the rate of decline in abundance used

to estimate mortality, I used data only from months over which these processes appeared low.

Results

Seasonal changes in YOY abundance and size structure

Young-of-the-year pinfish appeared first as post-larvae (9–12 mm) at shallow-water fixed seine stations during early November in Choctawhatchee Bay and early December in Tampa Bay and Charlotte Harbor, one to two months before mean temperatures were lowest (Fig. 2). In Choctawhatchee Bay and Tampa Bay, pinfish were first collected at deepwater trawl stations in the same month or one month after their initial appearance at seine stations (Fig. 2). In Charlotte Harbor, however, YOY were absent at trawl stations until January–March, one to three months after their first appearance at seine stations (Fig. 2).

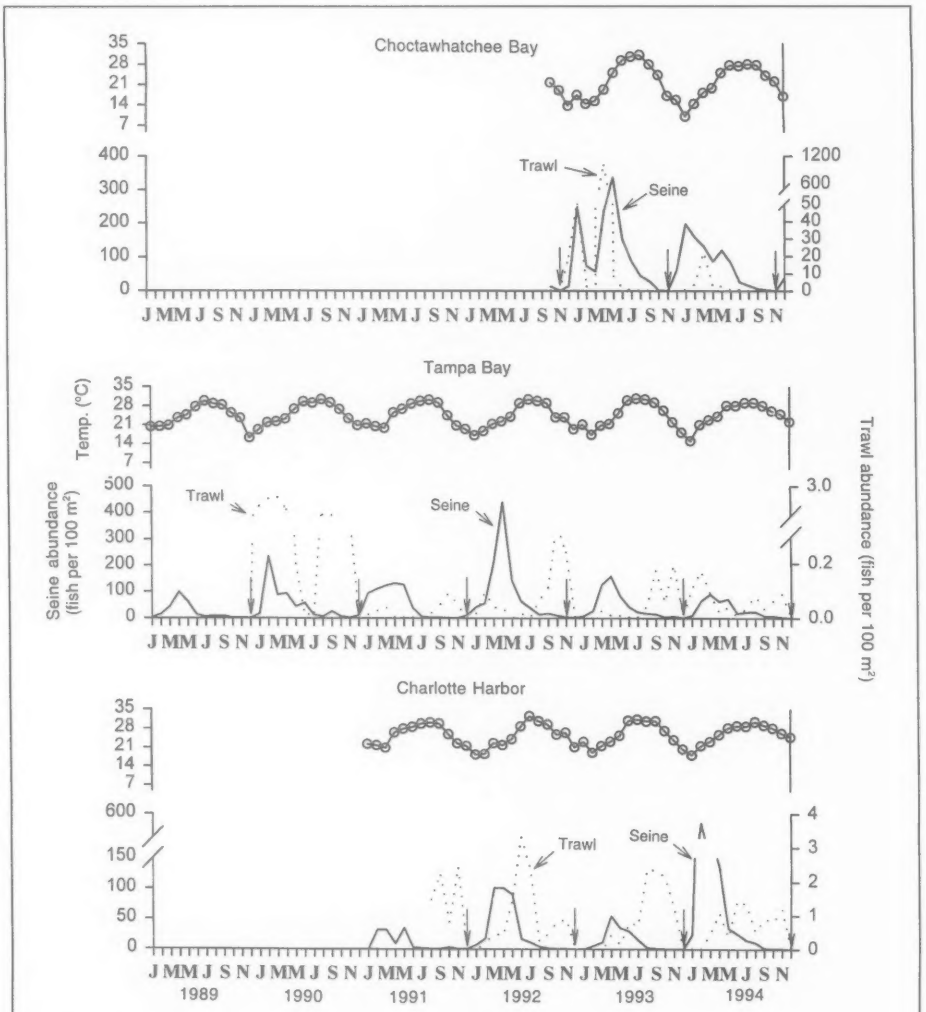
Choctawhatchee Bay
Tampa Bay
Charlotte Harbor
Temp. (°C)
Trawl
Seine
Seine abundance (fish per 100 m²)
Trawl abundance (fish per 100 m²)
J M M J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M J S N
1989
1990
1991
1992
1993
1994

Figure 2

Monthly relative indices of young-of-the-year pinfish abundance (no. of fish) and mean monthly water temperature at fixed seine and trawl stations from 1989–94 for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor. Vertical arrows indicate the month of initial recruitment.

Relative abundance at fixed seine stations peaked in January and May in Choctawhatchee Bay, generally during March–April in Tampa Bay and Charlotte Harbor, and declined thereafter (Fig. 2). In Choctawhatchee Bay and Tampa Bay, relative abundance at trawl stations generally followed fluctuations in seine catches, but usually peaked one to two months before the peak at seine stations (Fig. 2). A second peak in trawl abundance was observed in Tampa Bay from August to October (Fig. 2). In Charlotte Harbor, relative abundance at trawl stations peaked during June–September, two to five months after the peak in seine abundance (Fig. 2).

In all bays, smaller pinfish were generally captured at fixed trawl stations during November to March than at fixed seine stations (Figs. 3–5). Progression of the smallest fish size beyond the minimum size measured during the months of first capture indicated that settlement of postlarvae to fixed stations ended by March–April in all bays (Figs. 3–5). In Tampa Bay, catch proportions of YOY <40 mm decreased at trawl stations in March. In July, YOY >60 mm were captured in higher proportions at trawl stations in all bays than during the preceding months (Fig. 3–5). Pinfish overwintering at shallow-water seine stations in Choctawhatchee Bay tended to be smaller than those remaining at seine stations in Tampa Bay and Charlotte Harbor (Figs. 3–5).

Depth distribution

About 80% of the trawl catches of YOY pinfish in spring occurred in waters <3.1 m, <3.5 m, and <2.8 m in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor, respectively. Few fish (<1% of total catches) were captured in waters >5 m. The Kolmogorov-Smirnov test showed that cumulative frequency distributions for YOY pinfish depth were significantly different from those for trawl depth in all bays (Choctawhatchee Bay: D=0.51, n_{depth}=80, n_{fish}=34, P<0.001; Tampa Bay: D=0.44, n_{depth}=373, n_{fish}=76, P<0.001; Charlotte Harbor: D=0.48, n_{depth}=268, n_{fish}=59, P<0.001).

Factors influencing YOY spatial abundance

The final GLM's accounted for proportions of 0.33–0.44 of the total variation in spring catches, depending on bay system (Table 1). Pinfish abundance was associated with the presence of bottom vegetation in all bays (Table 1; Fig. 6A), with rivers (zone F) and zones near bay mouths in Tampa Bay (D and E) and

Table 1

Final results of the general linear model analyses of pinfish catches for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor in spring. Partial (type-III) mean squares are shown. * = P<0.05, **= P<0.01, and *** = P<0.001.

Location	Source	df	Mean square	F-value	r^2
Choctawhatchee Bay	Model	3	71.120	23.70***	0.436
	Year	1	0.097	0.03	
	Deployment	1	42.637	14.21***	
	Bottom vegetation	1	179.747	59.89***	
	Error	92	3.001		
	Corrected total	95	5.152		
Tampa Bay	Model	11	67.312	19.84***	0.334
	Year	5	14.041	4.14**	
	Zone	5	65.287	19.25***	
	Bottom vegetation	1	193.316	56.99***	
	Error	425	3.392		
	Corrected total	436	5.005		
Charlotte Harbor	Model	13	59.461	15.85***	0.421
	Year	5	24.823	6.62***	
	Zone	4	33.193	8.85***	
	Bottom vegetation	1	24.406	6.51*	
	Bottom sediment	1	43.380	11.56***	
	Salinity	1	62.795	16.74***	
	Temperature	1	22.778	6.07*	
	Error	283	3.752		
	Corrected total	296	6.198		

Charlotte Harbor (B and C) (Table 1; Fig. 6B), with beach seine sets in Choctawhatchee Bay (Table 1; Fig. 6C), and with mud bottom in Charlotte Harbor (Table 1; Fig. 6D). Young-of-the-year pinfish catches were related to salinity and temperature in Charlotte Harbor only (Table 1).

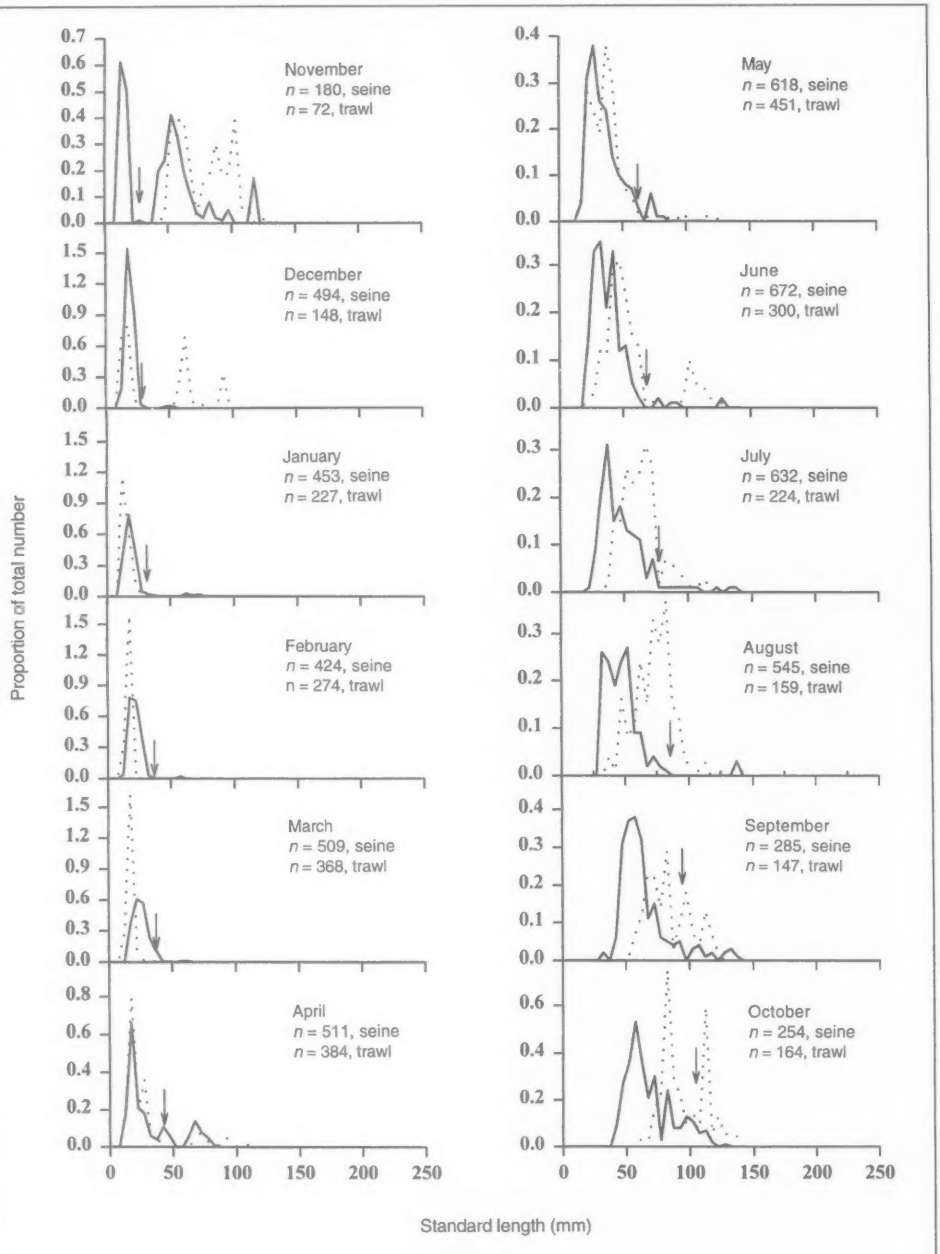

Figure 3

Monthly length-frequency distributions of pinfish captured at fixed seine (—) and trawl (· · ·) stations in Choctawhatchee Bay from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

Young-of-the-year pinfish abundance varied significantly between years in Tampa Bay and Charlotte Harbor (although not significant, year was included in the model for Choctawhatchee Bay to compute least squares means)(Table 1; Fig. 7). Pinfish abundance was also generally highest in Choctawhatchee

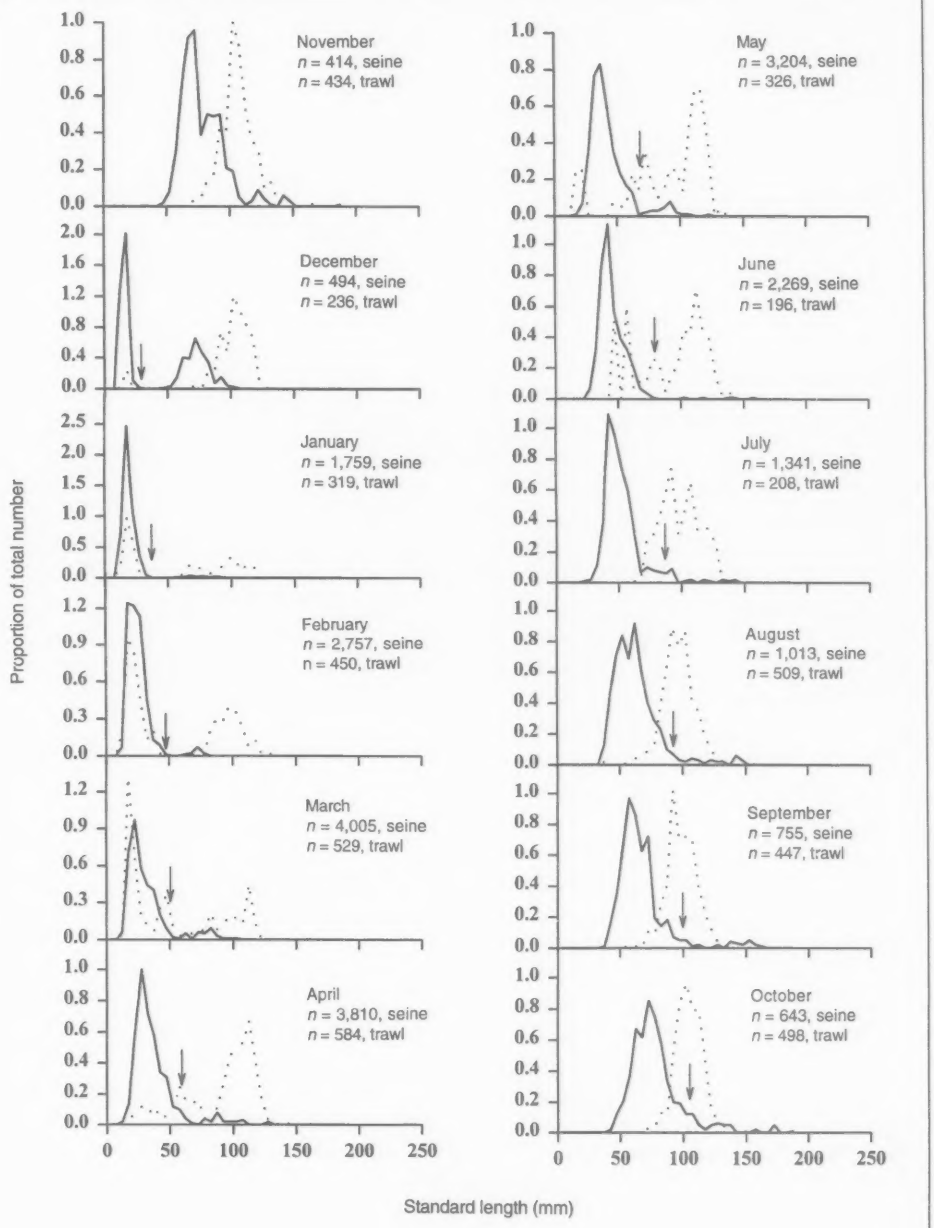

Figure 4

Monthly length-frequency distributions of pinfish captured at fixed seine(—) and trawl (· · ·) stations in Tampa Bay from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

Bay (range: 55.0–59.8 fish/haul), followed by Charlotte Harbor (5.5–50.4 fish/haul) and Tampa Bay (7.8–27.8 fish/haul)(Fig. 7).

Factors affecting YOY annual abundance

Relative abundance of YOY pinfish was significantly

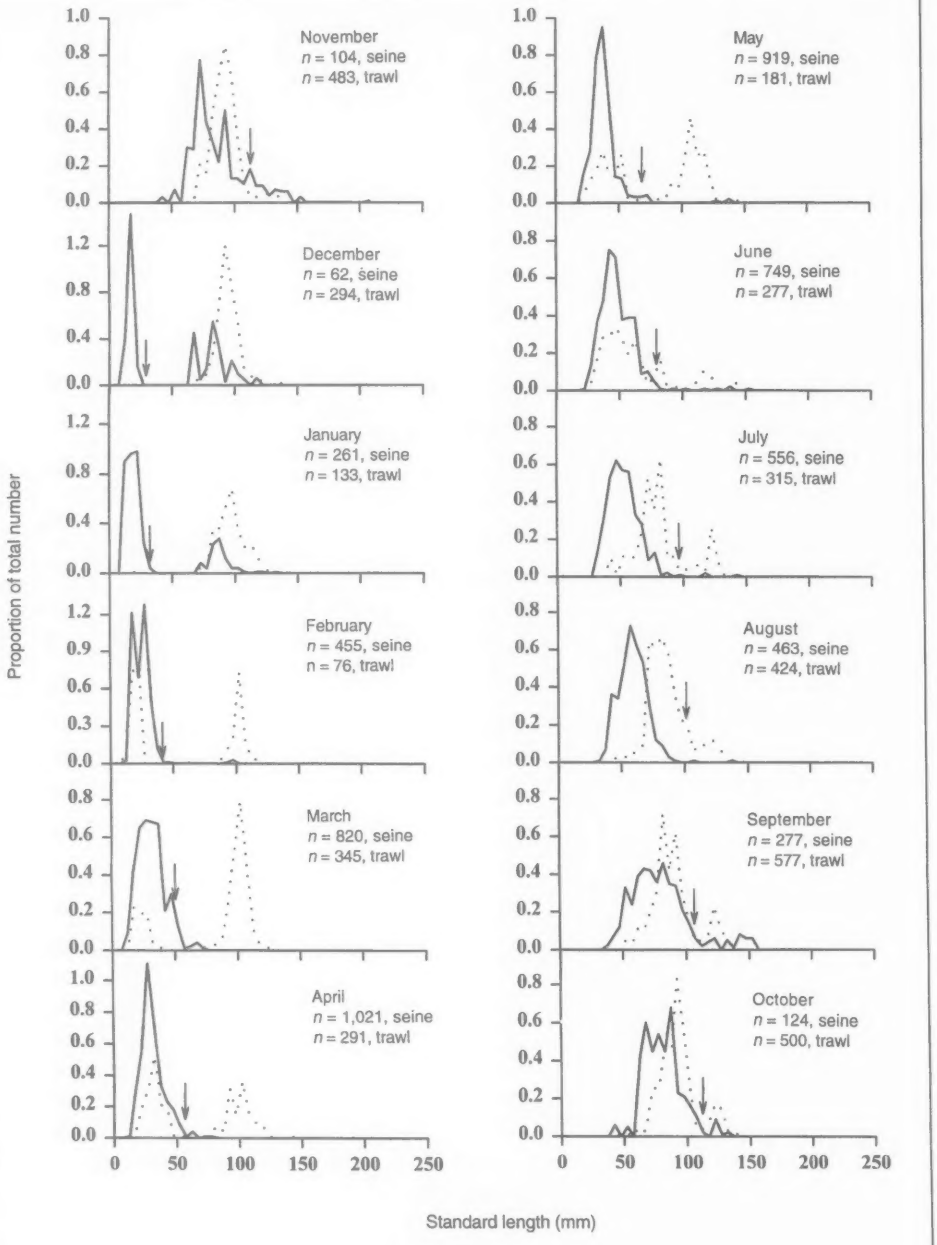

Figure 5

Monthly length-frequency distributions of pinfish captured at fixed seine(—) and trawl (· · ·) stations in Charlotte Harbor from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

and positively correlated with mean sea-surface temperatures in November (the month before first appearance) in Charlotte Harbor and with indices of adult abundance from 1988 to 1993 in Tampa Bay (Table 2).

Growth

Growth rates were estimated with mean length data from fixed seine stations only from April through July to minimize biases associated with potential movements of YOY pinfish. Year-class growth rates were similar among bays. Instantaneous growth coefficients ranged from 0.18 to 0.26/month for Choctawhatchee Bay, 0.06–0.21/month in Tampa Bay, and 0.14–0.26/month for Charlotte Harbor, indicating that monthly growth of YOY pinfishes is rapid during late spring and mid-summer months (Table 3). Comparisons among bays revealed no consistent interannual patterns in growth except from 1993 to 1994 when rates declined in all bays (Table 3).

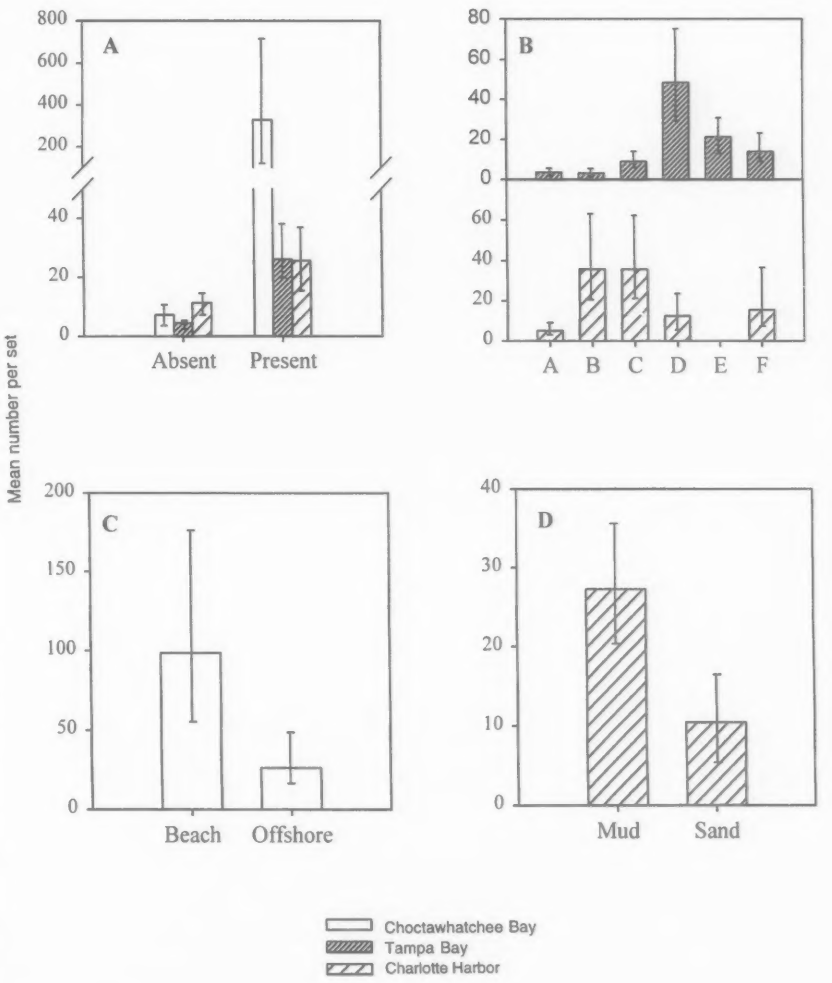

Figure 6

Least-squares means and 95% confidence intervals for main effects of (**A**) presence or absence of bottom vegetation, (**B**) zones, (**C**) deployment techniques, and (**D**) sediment type. Zones A–E encompass bay areas, whereas zone F encompasses rivers.

Mortality

The estimates of Z were calculated from the decline in indices of relative abundance at shallow-water fixed stations from May (month of secondary peak in abundance) to June for Choctawhatchee Bay, and April (month of peak abundance) to May for Tampa Bay and Charlotte Harbor. Relative abundance indices were averaged over all years prior to calculation in order to reduce the effects of interannual variability. Estimates of Z were 0.022/d, 0.021/d, and 0.023/d for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor, respectively (Table 4).

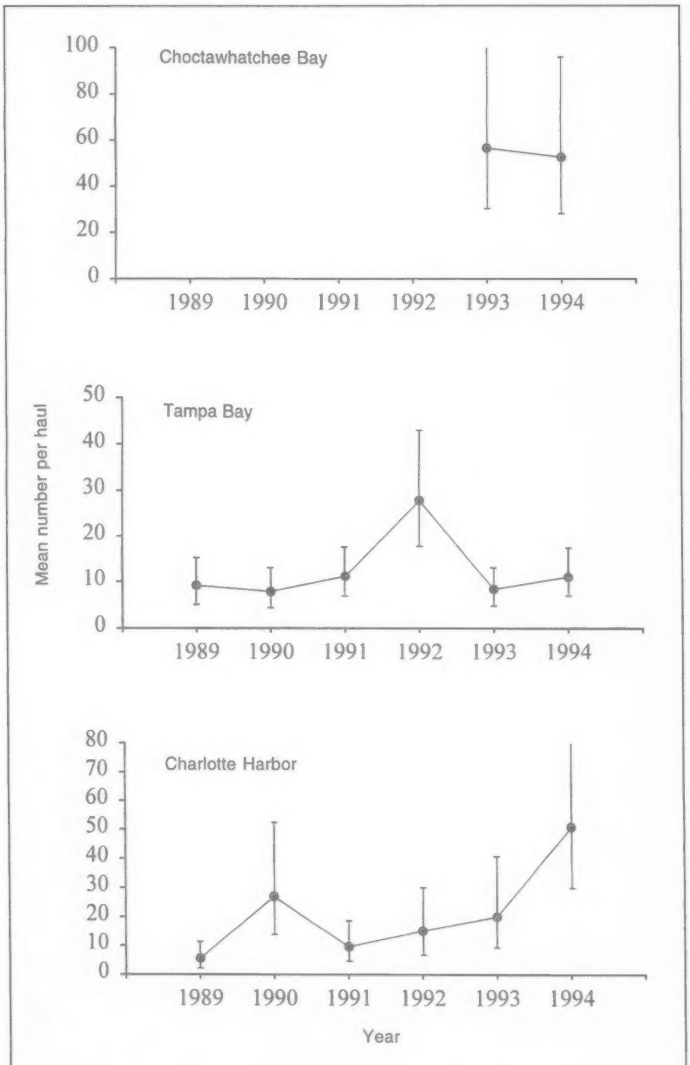

Figure 7

Annual indices of young-of-the-year abundance and 95% confidence intervals for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor from 1989 to 1994.

Discussion

Seasonal changes in YOY abundance and size structure

Pelagic pinfish larvae are transported from oceanic spawning areas and dispersed into estuaries via near-surface water currents (Darcy, 1985). After metamorphosis, postlarvae settle more or less near the bottom in estuaries (Hildebrand and Cable, 1938; Caldwell, 1957). Initial appearance of postlarvae (9–12 mm) and larger YOY (<28 mm) in shallow and deep water within a one-month period suggests pinfish settle to both areas in Choctawhatchee Bay and Tampa Bay. In Charlotte Harbor, settlement appears to occur first to shallow water, and then to deep water, because YOY pinfish were absent in trawls until 1–3 months after their first appearance at fixed seine stations. One explanation for these different patterns of settlement may lie with the bathymetry of each bay: more shallow-water area with seagrass beds (YOY pinfish are dependent on seagrass for protection from predators and food [Stoner, 1980; 1983]) is available in Charlotte Harbor (seagrass area=202 km^2) than in Choctawhatchee Bay (33 km^2) or Tampa Bay (83 km^2)(Sargent et al., 1995).

The occurrence of YOY pinfish mostly in water <3.5 m suggests that pinfish distribution is depth-restricted. The propensity of YOY pinfish to limit their depth is probably due to their dependence on seagrasses for cover (seagrasses are generally restricted to waters <2.3 m in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor [Durako[1]]), the distribution of pelagic and mobile epibenthic prey (Stoner, 1980), and light intensity (Gulbrandsen, 1996) (YOY pinfish must see their prey

[1] Durako, M. 1996. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL 33701-5095. Personal commun.

Table 2

Results of the Pearson product moment correlation tests for indices of recruit abundance from 1989 to 1994 versus mean sea-surface temperature during the months before and during initial recruitment from 1988 to 1993 and for indices of adult abundance from 1988 to 1993 for Tampa Bay and Charlotte Harbor. r is the Pearson product moment correlation coefficient, P is the significance probability, and n is the sample size. MRFSS = Marine Recreational Fisheries Statistical Survey.

		Tampa Bay		Charlotte Harbor		
	Month	r	P	r	P	n
YOY indices-temperature	October	–0.05	0.92	0.67	0.15	6
	November	–0.78	0.11	0.84	0.03	6
	December	0.15	0.78	–0.21	0.67	6
YOY indices–MRFSS adult indices		0.86	0.02	–0.15	0.78	6

Table 3

Regression statistics for mean length (ML) versus month (m) for young-of-the-year pinfish captured at fixed seine stations. The regression takes the form: $\mathrm{Ln}(ML) = \ln(L_0) + G \times m$ where $\ln(L_0)$ is the intercept and G is the instantaneous growth rate or slope. Only data from April to July were used. All slopes and intercepts were significantly different from zero.

Year	$\ln(L_0)$	SE	G-value	SE	r^2	n
Choctawhatchee Bay						
1993	2.03	0.217	0.26	0.038	0.956	4
1994	2.61	0.162	0.18	0.029	0.954	4
Tampa Bay						
1989	2.77	0.078	0.18	0.014	0.988	4
1990	3.53	0.116	0.06	0.021	0.818	4
1991	3.17	0.030	0.10	0.005	0.994	4
1992	2.64	0.072	0.20	0.013	0.992	4
1993	2.49	0.274	0.21	0.049	0.904	4
1994	2.98	0.175	0.14	0.031	0.905	4
Charlotte Harbor						
1991	2.38	0.095	0.26	0.017	0.991	4
1992	2.96	0.123	0.14	0.022	0.954	4
1993	2.46	0.243	0.21	0.043	0.920	4
1994	2.81	0.266	0.16	0.047	0.857	4

Table 4

Relative abundance (no. of fish/100 m^2) for April to June averaged over all years and estimates of total instantaneous mortality (Z) for young-of-the-year pinfish (*Lagodon rhomboides*) in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor. Data used to estimate Z are boldface.

Month	Choctawhatchee Bay	Tampa Bay	Charlotte Harbor
April	163.6	**164.2**	**97.2**
May	**228.2**	**88.5**	**48.9**
June	**119.2**	39.1	18.7
–Z	0.022	0.021	0.023

and therefore feed little at night [Kjelson and Johnson, 1976]).

Young-of-the-year pinfish that settle to deep water move to shallow-water areas in early spring. Evidence for this is the peak in trawl abundance of YOY pinfish in all years, followed by a rapid decline before the peaks in abundance at seine stations in Choctawhatchee Bay and Tampa Bay (Fig. 2). This movement to shallow water may be due to YOY seeking food and refuge from predators because it coincides with seasonal increases in seagrass biomass and prey abundance in shallow waters (Thoemke, 1979; Lewis et al., 1985) and because the shallow water and structural complexity of seagrasses may provide protection from predation (Savino and Stein, 1982; Stoner, 1983; Ruiz et al., 1993).

Young-of-the-year pinfish move from shallow-water to deepwater areas in mid- to late summer, and this movement appears to be related to YOY size. Evidence for this is the shift to larger sizes in trawls in July (Figs. 3–5) concurrent with increasing catches in trawls in Tampa Bay and Charlotte Harbor (Fig. 2). This movement may represent the initiation of their fall spawning migration (Caldwell, 1957; Hansen, 1970) because gonadal recrudescence begins as early as July (Cody and Bortone, 1992) and because the modal lengths observed in trawls in July were about 80 mm, which is the minimum size observed for YOY pinfish with developing gonads (Hansen, 1970).

Factors affecting YOY spatial abundance

Without meaningful, significant first-order interactions in the GLM analyses, the YOY abundance and main effect (zones, deployment technique, and bot-

tom type) relationships were difficult to assess. However, because pinfish abundance was associated with vegetation (seagrasses) in this and other studies (Stoner, 1980; Stoner, 1983), the significance of the main effects can be proposed in relation to seagrass distribution. Higher YOY pinfish abundances may have occurred in zones located near bay mouths because the largest areas of seagrass are located within these zones (Sargent et al., 1995). The absence of large expanses of seagrasses in Choctawhatchee Bay (Sargent et al, 1995) may have caused YOY pinfish to populate shallow-water beach areas abundantly to avoid predation (Ruiz et al., 1993). Because mud is commonly associated with seagrass beds in shallow-water areas of Charlotte Harbor (Mitchell[2]), higher abundances of YOY over mud may be expected.

It was surprising that more YOY pinfish were captured in Choctawhatchee Bay because there is less seagrass in this bay than in Tampa Bay or Charlotte Harbor (Sargent et al., 1995). Higher abundances of YOY pinfish may occur in Choctawhatchee Bay because *Halodule wrightii*, a thin-blade seagrass preferred by YOY pinfish for refuge and amphipod foraging (Stoner, 1982; 1983), occurred more frequently (62%) at vegetated sites in Choctawhatchee Bay than at vegetated sites in Tampa Bay (46%) and in Charlotte Harbor (40%).[3] The patchily distributed seagrass beds in Choctawhatchee Bay may also support higher abundances of pinfish than the continuously distributed seagrass beds in Tampa Bay and Charlotte Harbor because the ecotone between seagrasses and unvegetated areas may provide greater habitat complexity, offering protection from predators while providing close access to alternative feeding areas (Holt et al., 1983).

Factors influencing YOY annual abundance

Although this study is an exploratory analysis, the positive correlation between YOY abundance and sea-surface temperatures in Charlotte Harbor suggests that oceanographic or biological events that occur before settlement may be important factors contributing to the annual variability in pinfish abundance. Higher temperatures may favor increased hatching success (Postuma, 1971) or increased growth of larvae, or both (Hunter, 1981; Miller et al., 1985; Pepin, 1991), or they may affect transport mechanisms (Lasker, 1984; Rothschild, 1986). For pinfish, both explanations are plausible given that adults spawn in offshore Gulf waters.

Direct spawning stock-recruitment relationships are often masked by variability in recruitment (Fogarty et al., 1991). The lack of correlation between YOY and adult abundances in Charlotte Harbor suggests that temperature may be a more influential factor for this bay. The significant correlation between YOY and adult indices at such a low sample size does suggest that for Tampa Bay, the relationship may not be markedly masked, and identification of the actual spawning stock-recruitment patterns may be possible with additional years of data.

Growth

To compare growth rates for YOY pinfish from this study with those found for pinfish from Cedar Key, FL, Redfish Bay, TX, and the Laguna Madre, TX, I fitted the same growth equation to mean length data of YOY pinfish estimated from graphical plots shown in Caldwell (1957) for Cedar Key, Cameron (1969) for Redfish Bay, and Hellier (1962) for Laguna Madre, for April–July. Instantaneous growth rates were 0.10/month for YOY pinfish from Redfish Bay, TX, 0.17/month from the Laguna Madre, TX, and 0.25/month from Cedar Key, FL, indicating that growth in these bays was similar to growth of YOY pinfish in the three bays studied (Table 4). Similar growth rates were expected given that temperatures experienced by YOY pinfish among the Gulf coast estuaries were alike during the April to July growth period (Caldwell, 1957; Cameron, 1969; Hellier, 1962).

Mortality

Daily mortality of YOY pinfish in shallow-water areas of the three Florida estuaries was low. My estimates of mortality (0.021–0.023) were similar to those made for other estuarine-dependent species such as juvenile gulf menhaden (*Brevoortia patronus*) in Fourleague Bay, Louisiana (0.017–0.021)(Deegan, 1990), spot (*Leiostomus xanthurus)* in York River, Virginia (0.017) (Weinstein, 1983), and Atlantic croaker (*Micropogonias undulatus*) in Rose Bay, North Carolina (0.023) (Currin et al., 1984). Unfortunately, I could not estimate mortality of YOY pinfish in deep water because emigration and immigration appeared to occur continuously over the spring–summer period at fixed trawl stations.

In summary, YOY pinfish first appeared in shallow-water areas during November in Choctawhatchee Bay and during December in Tampa Bay and Charlotte Harbor. In Choctawhatchee Bay and Tampa Bay, they were captured in deep water within one month

[2] Mitchell, M. E. 1997. Florida Marine Research Institute, Charlotte Harbor Field Laboratory, 1481-A Market Circle, Port Charlotte, FL 33953. Personal commun.

[3] Percent occurrence for seagrasses was estimated from random sampling data in spring.

after their shallow-water appearance. In Charlotte Harbor, YOY pinfish were absent in deep water until 1–3 months after they first appeared in shallow water. Young-of-the-year pinfish were generally restricted to depths <3.5 m in all bays. Two general movements were evident: from deep water to shallow water in spring, and from shallow water to deep water in mid- to late summer, the latter movement being size-dependent. High abundances of pinfish were commonly associated with the presence of seagrasses. Despite differences in abundance among bay populations, growth and mortality rates of young-of-the-year pinfish were similar in all bays.

Acknowledgments

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Low-frequency acoustic measurements of Pacific hake, *Merluccius productus*, off the west coast of the United States

Redwood W. Nero
Charles H. Thompson
Richard H. Love

Naval Research Laboratory, Code 7174
Stennis Space Center, Mississippi 39529-5004
E-mail address for R.W. Nero:woody.nero@nrlssc.navy.mil

Abstract.—Low-frequency volume scattering measurements were conducted by the Naval Research Laboratory (NRL) on the upper slope, slope base, and abyssal plain along the U.S. west coast between the Strait of Juan de Fuca, Washington, and Cape Mendocino, California. Comparisons of swimbladder radii estimated from resonances with those estimated from fish lengths obtained from quasisynoptic National Marine Fisheries Service (NMFS) trawl catches of Pacific hake, *Merluccius productus,* strongly suggest that the major source of the low-frequency scattering were Pacific hake. Estimates of hake density from the NRL low-frequency measurements and the NMFS acoustic, midwater trawl survey on the slope gave comparable values of 195–439 kg/ha and 91–369 kg/ha respectively. However, NRL measurements, up to 50 km offshore of the outer limit of the NMFS survey, found densities of 270–300 kg/ha in layers peaking at 225 to 450 m depth. This finding suggests that high densities of hake may occur farther offshore of the traditional limit of NMFS surveys and at depths which may be difficult to survey with conventional fisheries sounders.

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Pacific hake, *Merluccius productus*, are the most abundant large midwater fish on the continental shelf and slope of the west coast of the United States during summer (Ware and McFarlane, 1989). Hake winter between Point Conception, CA, and Baja California. In spring they migrate northward to feed in the productive waters along the continental shelf from northern California to Vancouver Island. They remain in this area from May through October. The migration between the winter spawning grounds and the summer feeding grounds is size structured, i.e. related to fish length and optimum swimming velocity (Francis, 1983; Smith et al., 1992), with the larger fish swimming faster and farther. Large fish migrate farthest north to near Vancouver Island, smaller fish reach only as far as southern Oregon and northern California (Stauffer, 1985).

A midwater trawl fishery targets hake occurring in dense feeding aggregations along the shelf break in midsummer (Stauffer, 1985). Since 1977, the National Marine Fisheries Service (NMFS) has conducted a triannual acoustic, midwater trawl survey to determine hake distribution and abundance (Dorn et al., 1994). During the 1992 survey, NMFS integrated volume scattering with a high-frequency (38-kHz) echo sounder and corroborated fish identity and size with midwater trawls. Volume scattering was converted to fish biomass with a volume scattering to biomass regression (Dorn et al., 1994).

Coincident with the 1992 fishery survey, the Naval Research Laboratory (NRL) conducted an acoustic survey of volume scattering using a broad-band low-frequency measurement system (Thompson and Love, 1996). Because the NRL survey was conducted quasisynoptically with the fisheries survey, comparisons were possible between the two surveys.

Although echo sounders at relatively high frequencies (>20 kHz) are a standard tool in fisheries surveys (MacLennan and Simmonds, 1992), a broad-band low-frequency sound at the natural resonance of the population of fish swimbladders at depth have been used as an alternative tool (Holliday, 1972; 1977a). A variety of acoustic models has been developed to help predict and understand various aspects of this resonance (Anderson, 1950; Andreeva, 1964; Love, 1978; Stanton, 1989; Clay, 1991, Feuillade and Werby, 1994). With these models, the acoustic resonance of a population of fish swimbladders at depth can provide quantitative information about the fish population. The spectrum of the resonance is depen-

dent on swimbladder size, depth, and fish behavior (Sand and Hawkins, 1973; Love, 1993). The scattered sound at resonance is almost completely omnidirectional, independent of fish aspect (Feuillade and Werby, 1994). As a result, resonance measurements are useful for inferring the size and abundance of the swimbladders. An inverse solution of measured scattering levels can be used to generate a size-frequency distribution of swimbladders (Holliday, 1977b), from which fish size can then be inferred.

On the U.S. west coast, Pacific hake, measuring 45 cm in fork length and occupying depths of 50 to 500 m, are expected to be resonant near 500 to 1,500 Hz (Love, 1978). Midwater trawls show that no other large pelagic fish are as abundant as hake (Dorn et al., 1994). Other fishes expected to contribute to scattering are anchovy and mesopelagic fishes (Kalish et al., 1986). Both are much smaller than hake and at depths of 50 to 500 m should only contribute to scattering above 2 kHz.

This study reports on low-frequency volume scattering measurements from what are assumed to be Pacific hake at depths of 50 to 500 m over the continental slope off the Strait of Juan de Fuca and the Oregon–California coasts. Bioacoustic models are used to estimate the number and size of swimbladders at depth. These results are compared with estimates of swimbladder size and abundance obtained from quasisynoptic acoustic data and midwater trawl catches collected by the National Marine Fisheries Service.[1] A comparison of swimbladder size is problematic. Fish can either let their swimbladders compress according to Boyle's law during descent, or they can actively add gas to the swimbladder to maintain neutral buoyancy. In addition, the relation between fish size and swimbladder volume is also highly variable within a group of fish and is affected by feeding and other aspects of fish behavior (Ona, 1990). We consider these possibilities and suggest several hypotheses about the swimbladder behavior of Pacific hake.

[1] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. data.

Materials and methods

Measurements

The NRL low-frequency acoustic measurements were made from 14 to 29 August 1992 aboard the USNS *Wilkes* (T-AGS-33) in conjunction with a Naval Oceanographic Office (NAVOCEANO) survey. The NRL conducted measurements at 9 stations located on the continental slope and abyssal plain between the Strait of Juan de Fuca and Cape Mendocino (Table 1; Fig. 1). Stations 2 and 3 off the Washington coast were missed owing to heavy seas. Because we expected a north–south trend in the size composition of the hake, stations at similar latitude were grouped and named according to their proximity to geographic features: station 1—La Perouse; 4 and

Table 1

Volume reverberation stations conducted by the Naval Research Laboratory.

Station no.	Date	Time (local [h])	Day or night	Lat. N	Long. W	Bottom depth (m)
1	14 Aug	1836–1920	day	48°26'	126°20'	900
4	18 Aug	0120–0223	night	44°44'	125°04'	1,100
5	19 Aug	1325–1420	day	44°45'	125°42'	2,800
5	20 Aug	0145–0240	night	44°38'	125°43'	2,900
6	21 Aug	0000–0105	night	43°28'	125°40'	3,100
6	21 Aug	0925–1032	day	43°27'	125°38'	3,100
7	23 Aug	0025–0109	night	43°26'	125°04'	1,070
7	23 Aug	0858–0935	day	43°30'	125°06'	1,245
8	24 Aug	0905–0936	day	42°18'	124°54'	1,025
9	25 Aug	2212–2248	night	42°19'	125°40'	2,800
9	26 Aug	0856–0927	day	42°23'	125°39'	2,800
10	27 Aug	0925–1001	day	40°15'	125°35'	2,400
11	28 Aug	0117–0200	night	40°04'	125°09'	1,465
11	29 Aug	0931–1006	day	40°03'	125°08'	1,500

5—Heceta North; 6 and 7—Heceta South; 8 and 9—Sebastian; and 10 and 11—Mendocino.

Just prior to the NRL survey, NMFS conducted a high-frequency acoustic-midwater trawl survey of Pacific hake. The survey began just south of San Francisco and ended off Cape Scott, Vancouver Island (Dorn et al., 1994). Generally, trawls were located inshore of the NRL stations. The NRL and NMFS surveys were separated by 43 days in the south (station 11, trawl 8), but only 5 days in the north (station 1, trawl 45)(Fig. 1). The NMFS survey provided information on fish size and abundance that could be compared with the results of the low-frequency acoustic analysis. Comparisons were restricted to midwater trawls located close to the NRL stations within each of the above named latitudinal regions. A north–south trend in fish size was evident, although a gap occurred in the size distributions between 38 and 40 cm (Fig. 2). Trawls appeared to catch fish on either side of this gap; only a few trawls contained both size classes. This finding suggests that, at sea, different size classes remain spatially separate (Fig. 1).

The NRL sound scattering measurements used an explosive sound source and a directional acoustic receiver. A 0.23-kg TNT charge detonated at 0.5 m depth provided a high source level over a wide frequency range. The shallow detonation depth allowed the gas bubble created by the explosion to vent to the surface and prevented the multiple sound pulses caused by bubble oscillations characteristic of charges detonated at greater depth. Measurement sequences consisted of 4 to 6 shots over a 30-min period. Because the ship typically drifted at 1–2 knots, the distance over which data were collected was on the order of a mile.

The acoustic receiver used for these measurements consists of a thirty-two element line hydrophone, 0.9 m long, mounted along the axis of a conical reflector that had a height of 0.9 m and an open base with a diameter of 1.8 m. The purpose of the reflector was to map an annular area of the opening to each hydrophone element for sound entering the reflector parallel to the axis and to decrease sensitivity to sound entering the reflector from other directions. The receiver was originally designed for use at frequencies between 2.5 and 20 kHz. By varying the number of active hydrophone elements, the receiver's 3-dB beam width can be maintained between 10° and 20° in that frequency range. The eight elements nearest the vertex of the cone form a 45-cm aperture and are used for frequencies from 10 to 20 kHz. By doubling the active length with eight additional elements, a 90-cm aperture is formed that can be used for frequencies between 5 and 10 kHz, and all 32 elements form a 180-cm aperture that can be used below 5 kHz. Between 2.5 and 5 kHz, measured beam patterns of the receiver show a main lobe with shape and 3-dB beam width similar to the main lobe of theoretical beam patterns (Urick, 1983) for a plane circular array 1.8 m in diameter, whereas the side lobes are lower than those for a plane circular array. Below 2.5 kHz, the main beam widens beyond 20°, reaching 38° at 1,600 Hz, 58° at 800 Hz, and 74° at 500 Hz.

Received signals from each TNT shot were amplified, high- and low-pass filtered

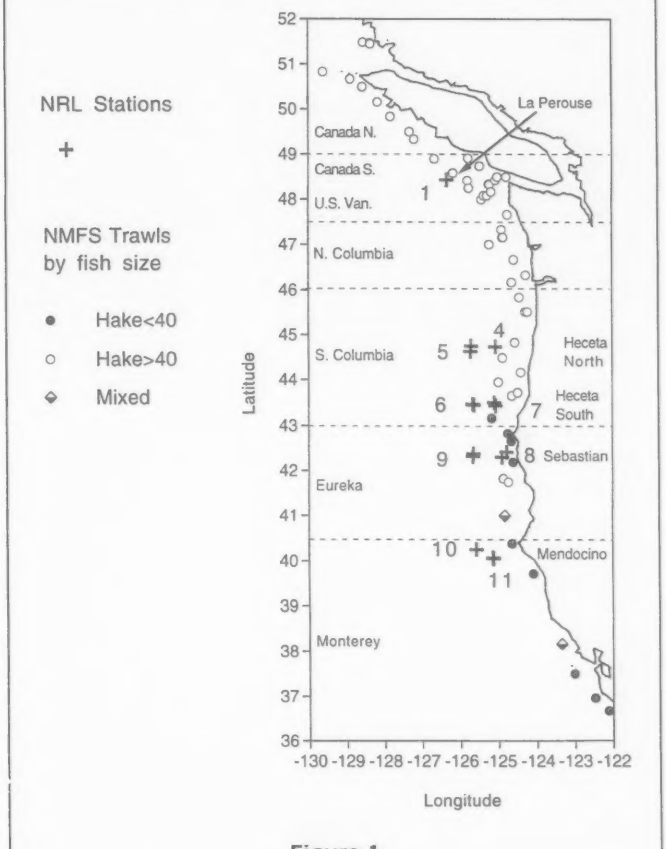

Figure 1

Map of the U.S. west coast showing Naval Research Laboratory (NRL) stations and locations where pertinent National Marine Fisheries Service (NMFS) midwater trawls were undertaken.

at 400 and 6,000 Hz, respectively, digitized at a 20-kHz sampling rate, and stored. Digitally stored signals were subsequently filtered into 21 1/6 octave bands from 500 to 5,000 Hz and amplitude versus time envelopes calculated for each band. There was little variation between shots in a sequence. Envelopes of all shots in a sequence were averaged to obtain a single set that was representative of scattering during that sequence, and this averaged data was used to calculate volume scattering strength, S_v, the scattering strength of a unit volume of water, as a function of depth. Data were displayed as 2-dimensional images showing S_v in dB on a color scale as a function of frequency and depth. Scatterer depths were determined from the S_v images; integration over these depths produced a series of layer scattering strength (S_L) versus frequency curves. On the basis of the distinct nature of the S_L curves, scatterers were assumed to be swimbladder-bearing fish. Hence, S_L curves were used to determine swimbladder size with a swimbladder scattering model. Fish swimbladders are not spherical, nonetheless their size may be conveniently expressed in terms of equivalent spherical radii (ESR) (i.e. the radii of spheres of equivalent volume). Thus ESR can be derived independently from acoustic data and trawl data and compared to evaluate each method for assessing population statistics.

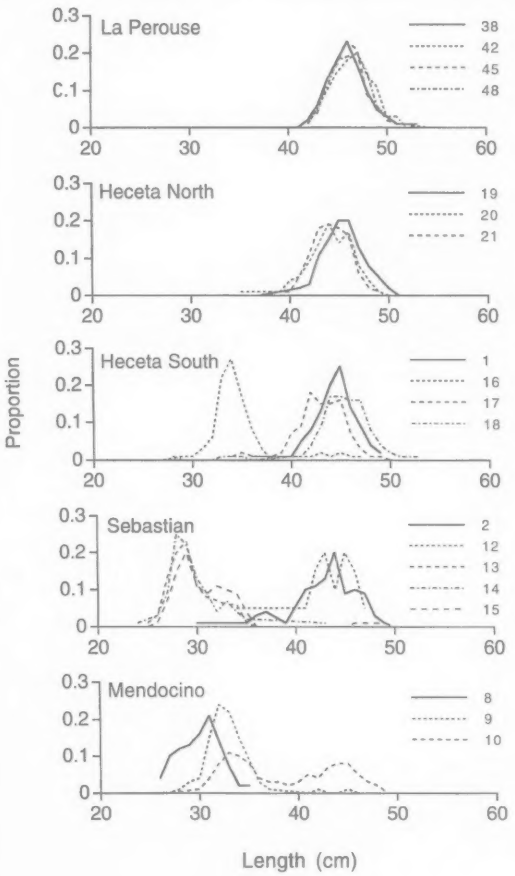

Figure 2

Length of hake taken in the 1992 NMFS acoustic-midwater trawl survey. Lengths are shown for trawls grouped by geographic region. Numbers indicate NMFS trawl number.

Inverse solution

The ESR of the scatterers were obtained from the S_L curves of the acoustic data with the nonnegative least squares solution of

$$\mathbf{S} = \sigma \mathbf{n}, \tag{1}$$

(Holliday, 1977b) for $\mathbf{n}$, a column vector containing the number of scatterers in each of p size classes of swimbladder radii. $\mathbf{S}$ is a column vector of measured layer backscattering cross sections σ_{bs_L} ($S_L = 10 \log \sigma_{bs_L}$) for the q frequencies at which measurements were made. The matrix σ is of dimension $q \times p$ and contains individual backscattering cross sections σ_{bs_i} that are calculated over each of the $q = 21$ measurement frequencies (1/6 octaves from 500 to 5,000 Hz) and $p = 18$ semilogarithmically spaced radii (r=0.25, 0.3, 0.35, 0.4, 0.45, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.2 1.4, 1.6, 1.8, 2.0, 2.25, and 2.5 cm) with a model of swimbladder resonance (Eq. 3 below). In solving Equation 1, the number of measurement frequencies varied from station to station depending on data quality, with from 4 to 6 of the lower 1/6 octaves excluded. This variation was usually due to lower-frequency data that were low level and affected by noise. The inverse solution was also restricted to exclude radii smaller than the radius expected to be resonant at 5,000 Hz at the depth of each layer. These radii were calculated with the subsequent Equation 4 for the resonance frequency, f_0. The quality of the inverse solution of Equation 1 for $\mathbf{n}$ was examined by comparing the original data, $\mathbf{S}$, to an estimate of the layer strength obtained from the forward calculation $\hat{\mathbf{S}} = \sigma \mathbf{n}$.

Solution of Equation 1 above assumes that the σ_{bs_L} are the backscattering cross sections of a unit horizontal area of a layer of dispersed acoustically noninteracting scatterers, such that

$$\sigma_{bs_L} = \sum_{i=1}^{\Phi} \sigma_{bs_i}, \tag{2}$$

where σ_{bs_i} is the backscattering cross section of the i^{th} scatterer and Φ is the number of individuals within a 1-m^2 vertical column that extends over the depth of the layer. At some stations, usually at night, several layers were evident. In these cases, Equation 1 was solved for each individual layer, and the subsequent distributions of ESR were summed.

Swimbladder model

The matrix σ of individual backscattering cross sections σ_{bs_i} was calculated with Love's model (1978) which models a fish swimbladder as an air-filled viscous spherical shell. The acoustic cross section in the back-scattered direction, σ_{bs}, for a single swimbladder of radius r is given by

$$\sigma_{bs} = \frac{r^2}{\left(\frac{f_0^2}{f^2 H^2} + \left(\frac{f_0^2}{f^2} - 1 \right)^2 \right)}, \tag{3}$$

where σ_{bs} is in m^2;
r is in m;
f = the insonifying frequency in Hz;
f_0 = the swimbladder's monopole resonance frequency in Hz; and
H = a damping factor.

The resonance frequency is

$$f_0^2 = \frac{3\gamma_a P}{4\pi^2 r^2 \rho}, \tag{4}$$

where γ_α = the ratio of specific heats of air (γ_α=1.4);
P = the ambient pressure in Pa; and
ρ = the density of fish flesh in kg/m^3.

The damping factor is

$$\frac{1}{H} = \frac{2\pi r f^2}{f_0 c} + \frac{\xi}{\pi r^2 f_0 \rho}, \tag{5}$$

where c = the speed of sound in water in m/sec; and
ξ = the viscosity of fish flesh in Pa sec.

Love's model includes a term in Equation 4 that accounts for the effects of swimbladder wall tension on f_0 and a thermal damping term in Equation 5. However, Love (1978) shows that these terms are negligible for the present case, therefore they were omitted for clarity. The physical properties of fish used here were taken from Love (1978): ρ = 1050 kg/m^3 and ξ = 50 Pa sec.

Swimbladders are not spherical but resemble prolate spheroids or cylinders with major-to-minor axis (length-to-diameter) ratios up to 10. However, it has been shown that spheroidal and cylindrical air bubbles have only a slightly higher resonance frequency than spherical bubbles (Weston, 1967; Feuillade and Werby, 1994; Ye, 1997). Love's model with Weston's correction to the resonance frequency has recently been used successfully to examine scattering from commercial-size fish in several ocean regions (Love, 1993; Thompson and Love, 1996) and what are presumed to be deep-water grenadiers off Oregon (Nero et al., 1997).

To model hake for this study, we assumed the swimbladder to be a prolate spheroid with a major-to-minor axis ratio of 8. This assumption is reasonable based on our at-sea measurements on Pacific hake (see below) and reported measurements on 13 pollack, *Pollachius pollachius,* from the North Atlantic (Foote, 1985), both of which gave major-to-minor axis ratios near 8. The resonance frequency of such a spheroid is about 20% higher than for a sphere of equal volume (Weston, 1967); this correction factor was taken into account by increasing f_0 given in Equation 4 by a factor of 1.2. Recently, Feuillade and Werby (1994) have shown that the broadside target strength of such spheroids is about 0.5 dB less than that of a sphere. Because this difference is well within the expected error of our measurements, it was not incorporated into our model calculations.

Fish length and bladder size

We made direct comparisons of ESR derived from the NRL acoustic data with estimates of ESR from the lengths of fish obtained in NMFS trawls. However, the process of deriving swimbladder size from fish length is problematic. Because one of the primary functions of a swimbladder is to act as a hydrostatic organ, making a fish neutrally buoyant, one can assume ratios of swimbladder volume to fish volume near 0.05 (Jones and Marshall, 1953). However, many fish are frequently less than neutrally buoyant. In addition, food and gonadal products can crowd the abdominal cavity and reduce swimbladder volumes. Repeated measurements indicate values near 0.03 are common for gadoids (Foote, 1985; Ona, 1990) but that they are highly variable (Sand and Hawkins, 1973; Jones and Scholes, 1985; Foote, 1985; and Ona, 1990). Our field measurements on five hake

caught by angling at the surface at night gave values ranging from 0.03 to 0.09 (rough approximations from fish length and swimbladder dimensions). Because these fish had ascended several meters to take artificial bait at the surface, we chose to use the more accurate determination of 0.03 for pollack and saithe, *Pollachius virens,* calculated from data in Foote (1985). For converting fish length to weight we used $W = 0.0057L^{3.026}$, determined from lengths and weights of hake captured in the 1992 NMFS trawls, males and females combined.

Calculated swimbladder size distributions were modified to account for two sources of variability expected in the natural hake population. First, for variability of bladder radii due to the above mentioned effects of food and gonadal products, we approximated the distribution of swimbladder volume to fish volume as follows: 30% of the fish had the mean value of 0.03 whereas 10% of the fish had swimbladders 50% smaller, 20% had swimbladders 25% smaller, 30% had swimbladders 25% larger, and 10% had swimbladders 50% larger than the mean. These values were based on rough approximations of information contained in Ona (1990). Second, for variability in the fish weight (W) to length (L) relationship, we approximated a normal distribution of W on L, where 20% of the fish had the mean W given by the regression equation $W = 0.0057L^{3.026}$, and 17% were 10% heavier (lighter), 12% were 20% heavier (lighter), 7% were 30% heavier (lighter), and 4% were 40% heavier (lighter) than the mean.

Abundance and biomass estimates

Abundance data for hake were determined by summing **n**, the column vector of fish number to obtain Φ. Biomass was determined by summing the product of **n**, the column vector of fish number, and the expected weight of each fish (r to L and L to W, relationships above). Biomass values were averaged for the NRL stations, grouped according to NMFS fisheries assessment regions: Canada South (Sta. 1); Southern Columbia (Sta. 4, 5, 6, and 7); and Eureka (Sta. 8, 9, 10, and 11) and compared with reported surface biomass of hake obtained from the NMFS high frequency acoustic survey (Fig. 10 in Dorn et al., 1994).

Results

Volume scattering data

Stations 1 (Fig. 3), 7 (Fig. 4), and 11 (Fig. 5) were selected to show representative volume scattering because they are on the slope in 900 to 1500 m of water and encompass the latitudinal range of stations covered by the NRL survey (Fig. 1). Stations 7 and 11 had day and night data; station 1 had only day data. In each image, S_v is shown as a function of frequency and depth. For shallow stations, bottom echoes are black. In all images, what appears to be intense scattering near the surface is actually the direct blast from the shot and close-in surface scatter. Most stations show three layers of scatterers.

All stations had a strong scattering layer between 100 and 500 m both day and night. During the day the layer was strongest at 200 to 300 m with a resonance peak at about 1,000 Hz. This layer becomes progressively deeper to the south, being centered at 200 m at station 1, 220 m at station 7, and 320 m at station 11. This layer was presumed to be composed of Pacific hake on the basis of a prior consideration of the most likely abundant scatterers.

A second layer occurred at about 50 to 200 m at night and scattered sound at 3 to 5 kHz, frequencies well above the strongest (peak) scattering from the hake (Figs. 4B and 5B). The depth and frequency of occurrence of this layer matches the findings of Kalish et al. (1986) who provide a detailed study of the composition and scattering strengths of mesopelagic fish off Oregon. Therefore, we conclude this nighttime layer to be mesopelagic fishes that, during the day, should be deeper (near 200 to 300 m), resonant above 5,000 Hz, and not detectable by our measurements. This is supported by weak daytime scattering above 4,000 Hz at 250 m (Fig. 5B), which may be the low-frequency end of this daytime mesopelagic layer.

A third layer, beginning at about 1,000 m and extending to the end of the data record was evident in all data extending beyond 1,000 m. On the basis of this layer's resonance near 2,000 Hz and its location in depth, Nero et al. (1997) concluded that this scattering layer was caused by pelagic grenadiers. In subsequent analysis we considered only the low-frequency scattering from the hake—those scattering layers that are above 600 m and have a resonance below 2 kHz.

The acoustic resonance of the hake swimbladders is evident in the layer strength data for both day and night (points, Figs. 6 and 7). During the day, the majority of the scattering occurred in a fairly narrow depth range (Figs. 3–5); therefore only one set of layer strength data was calculated at each station (Fig. 6). During the night, the fish were more dispersed, and therefore the hake layer was separated into sublayers, and layer strengths were calculated for each (Fig. 7). Day layer strengths in the north at station 1 peaked at a slightly lower frequency (1,050

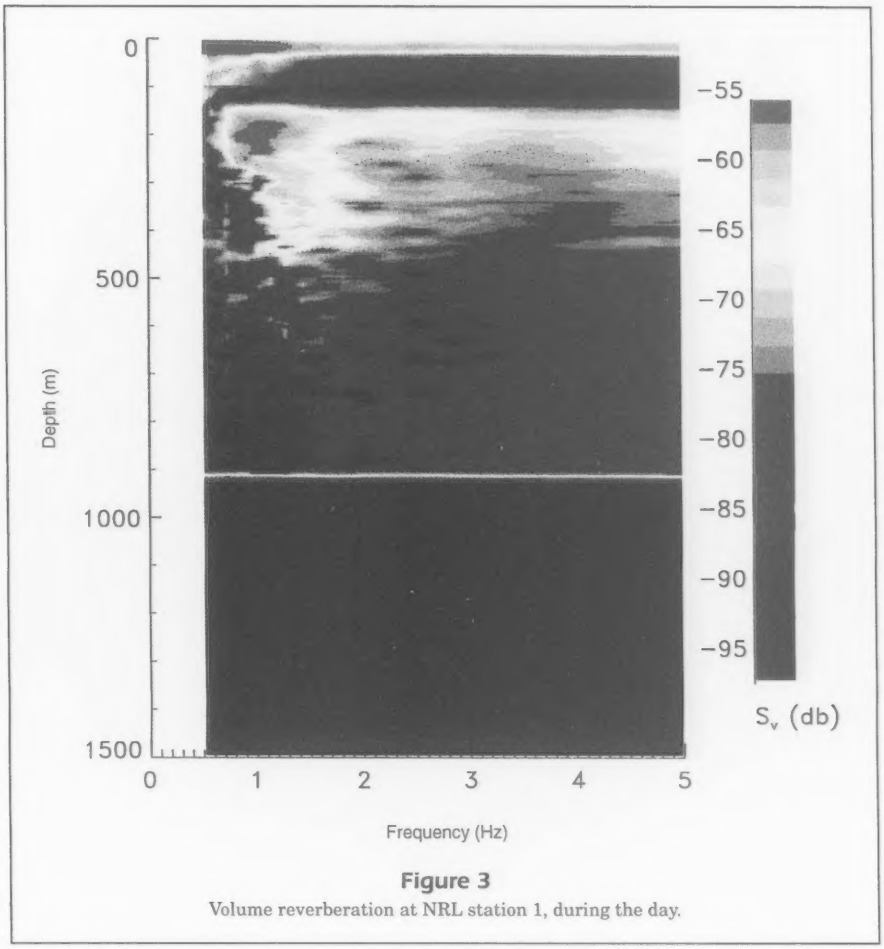

Figure 3
Volume reverberation at NRL station 1, during the day.

Hz) than at station 11 in the south (1,400 Hz). At night the resonance peaks of the individually integrated layers differed, with the peaks of the shallow sublayers occurring at about 1,000 Hz and the resonance peaks of the deep sublayers occurring at about 1,500 Hz.

Bladder size and number

The inverse analysis resulted in the determination of a distribution of ESR for each station grouped by geographic area (Fig. 8). The inversion gave an almost exact fit to the scattering data (curves and points in Figs. 6 and 7) indicating that the estimates of the distributions of ESR were quite good. Overall, the largest radii are near 2.2 cm, peaks occur between 1.2 and 1.8 cm, there is a dip at 0.8 cm, and smaller peaks occur between 0.5 and 0.7 cm. With the weight-length regression for hake given earlier, a swimbladder volume to fish volume ratio of 0.03, and if variabilities in either are ignored, $L = 28r$. Thus, the inversion tells us that, if the larger scatterers are hake, they are between 22 and 62 cm long with the greatest number between 34 and 50 cm (ignoring that variabilities increase the size range slightly). Figure 2 indicates that NMFS caught hake between about 25 and 55 cm length, with the greatest number between 28 and 46 cm length. Hence, we believe the estimated size range agrees well with trawl data, and we feel confident in our assumption that the scatterers with ESR of 0.8 to 2.2 cm are, indeed, Pacific hake.

Scatterers with ESR below 0.8 cm were present at all stations with the greatest numbers occurring between 0.5 and 0.7 cm (Fig. 8). According to their ESR, these fish are probably a mixture of mesopelagic fish and northern anchovy. This is consistent with findings of Kalish et al. (1986) who caught several spe-

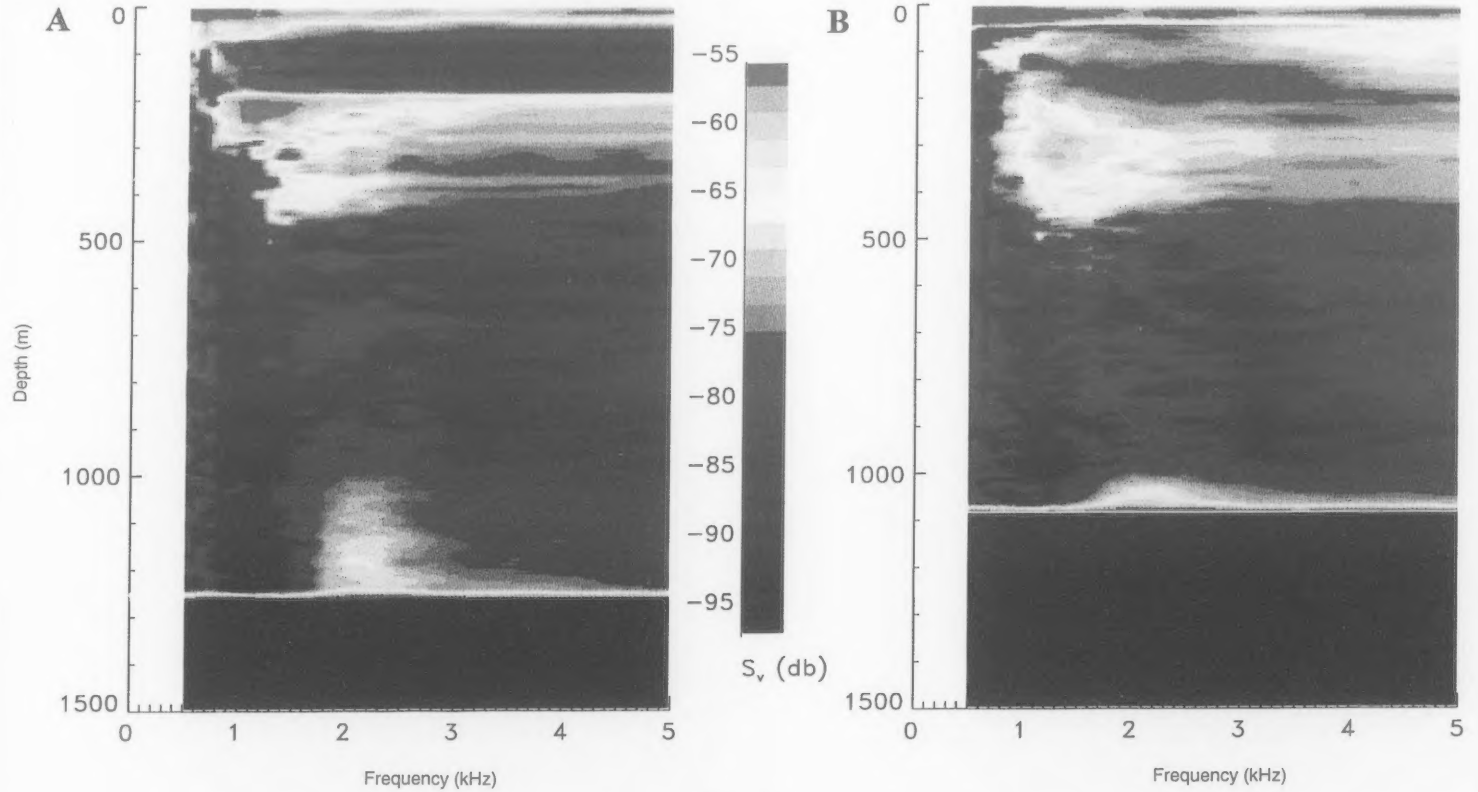

Figure 4

Volume reverberation at NRL station 7; (**A**) during the day, and (**B**) during the night.

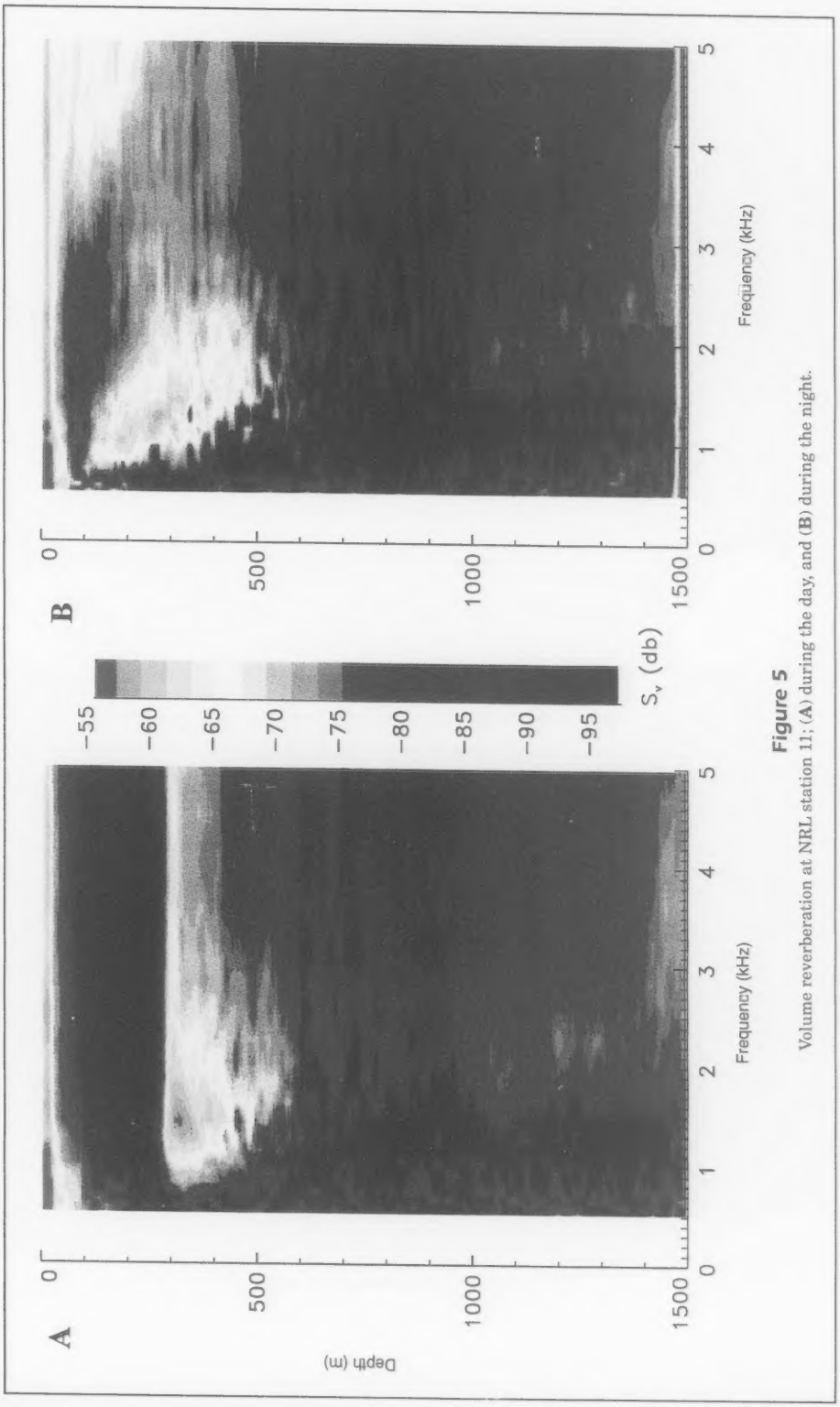

Figure 5

Volume reverberation at NRL station 11; (**A**) during the day, and (**B**) during the night.

cies of mesopelagic fish (*Symbolophorus californiensis*, *Tarletonbeania crenularis*, and *Diaphus theta*) and northern anchovy (*Engraulis mordax*) off the coast of Oregon at depths corresponding to our acoustic layer depths and had ESR between 0.1 and 0.7 cm. Thus, we expect that the fish with ESR between 0.25 and 0.7 cm in the present study are most likely these species.

For a more complete comparison of the trawl and low-frequency acoustic data, the lengths of hake caught in trawls were converted to ESR by using the previously mentioned weight-length regression and the swimbladder-volume-to-fish-volume ratio. The conversion included the variability in both relationships so that these ESR would be equivalent to the measured ESR. Figure 9 shows the resulting trawl estimates of ESR. The estimated distributions agree well with the measured ESR in the north at La Perouse, Heceta North, and Heceta South but not at the southern stations of Sebastian and Mendocino. The trawl data show a clear north–south trend in fish size (Figs. 2 and 9), whereas the acoustic data (Fig. 8) indicate that ESR, and presumably hake body size, do not change with latitude. The NRL low-frequency acoustic measurements did not show the same north–south trend in fish size that was apparent in the trawl data.

A summary of the number of swimbladders for small, 0.25–0.7 cm, and large fish, 0.8–2.5 cm, determined from the low-frequency acoustic data is given in Table 2, which includes information on the peak depth at which scattering occurred and the depth range of each layer. The density of small fish was much greater at night than during the day because these fish probably migrated to below 200 m during the day where they were resonant well above 5 kHz. For the large fish (presumably hake), at all stations where day–night measurements were made, densities were determined to be higher during day than at night. These higher daytime densities likely occurred because some hake migrated above 50 m depth at night and were missed because of the signal saturation caused by the explosion. (Measurements with an upward-looking system indicated that hake migrated to within several meters of the surface at some stations at night[2]).

The quasi-synoptic NRL and NMFS measurements provided an opportunity to compare two independent measures of the surface density of hake for several large regional areas of the U.S. West Coast. Only daytime density estimates were compared because data suggested that hake near the surface at night were missed by NRL acoustic measurements. Daytime surface density estimates for both surveys are given in Table 3. The estimates differ most for Canada South (NRL station 1) where NRL saw an abundance of fish over bottom depths near 1,000 m whereas the NMFS acoustic-midwater trawl survey saw approximately 1/4 that number. NRL station 1 was within the region covered by the NMFS survey tracklines (Dorn et al., 1994) and was sampled by NRL 5 days

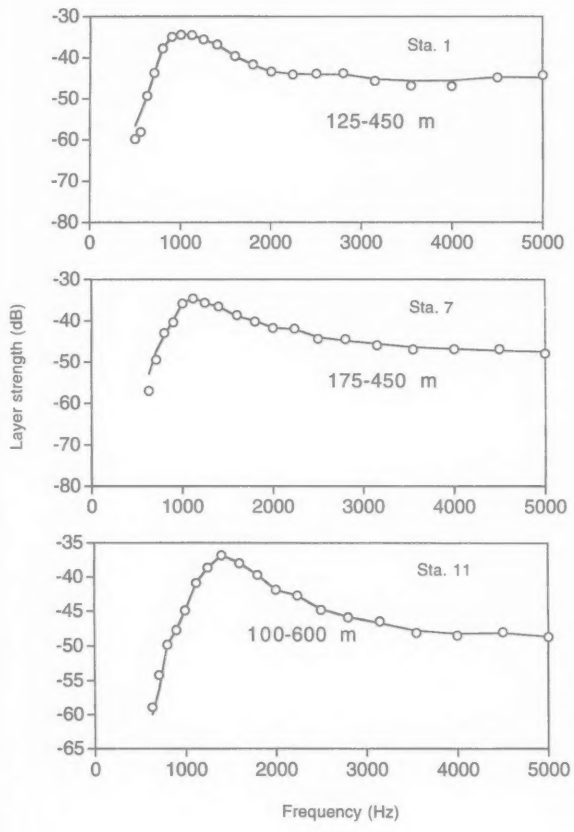

Figure 6

Layer strength data (open circles) for the daytime. Curves show inverse analysis fit to the data.

[2] 1992. Naval Oceanographic Office (NAVOCEANO), Acoustics Div., Stennis Space Center, MS, 39522-5001. Unpubl. data.

after the NMFS survey. At all other NRL inshore stations, densities were similar to the NMFS survey estimates. At all offshore NRL stations, densities remained high. Comparisons between the offshore NRL station data and the NMFS data were not possible because the NMFS survey did not extend beyond bottom depths of approximately 1,200 m. The offshore NRL measurements, approximately 50 km beyond the NMFS survey, gave densities as high as 300 kg/ha in layers at 300 to 400 m depth.

An examination of swimbladder behavior in hake was conducted on the NRL data by determining the relation between the acoustically measured swimbladder radii and depth for all stations (Fig. 10). In this analysis, it was assumed that hake at one station do not exhibit a size-dependent stratification in the water column. At night, hake were spread throughout the water column, allowing estimates of average ESR for several distinct layers at some stations. During the day, the hake were in a more compact single layer, resulting in only one estimate.

In Figure 10 curve, "A" depicts the shape of the relation between swimbladder radii and depth that is expected if the gas volume changed according to Boyle's Law and the bladder radius decreased with increasing depth. If hake maintain a near constant volume of gas in their bladders by adding or removing gas, then they would have a constant swimbladder radius, as depicted by line "B" in Fig. 10. There are no clear trends in the data. However, several weak relationships are worth noting. First, data taken from less than 100-m depth at stations 5 and 7 show unusually small radii suggesting some size-dependent stratification. Excluding these two values gives a weak but significant correlation for the remaining data (correlation coefficient=–0.373). In addition, two sets of data, from stations 9 and 11, and possibly from station 5, exhibit a decrease in bladder radius with depth. Stations 6 and 7 show an increase in radius with depth whereas station 4 shows maximum radius at middepth.

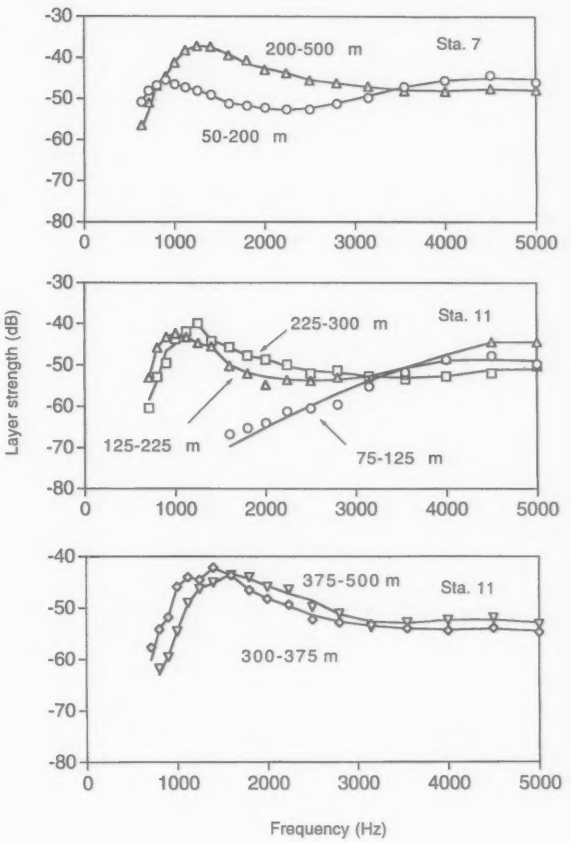

Figure 7

Layer strength data (symbols) for the nighttime. Curves show inverse analysis fitted to the data (note: no data were collected during night at station 1 and station 11 is separated into two panels for clarity).

Discussion

Pacific hake are believed to be the main cause of midwater scattering at frequencies of 1–2 kHz along the continental shelf and slope of the west coast of the United States (Figs. 6–7). No other large bodied midwater fishes are as abundant as hake (Ware and McFarlane, 1989). In addition, hake made up 97% of the catch in midwater trawls taken during the NMFS triennial acoustic-midwater trawl survey in the summer of 1992.[3] Other small fishes, mesopelagic fish, and northern anchovy may be abundant but will resonate well above 2 kHz. They are believed to be the source of scattering above 3 kHz in the upper 200 m at night (Fig. 7).

[3] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

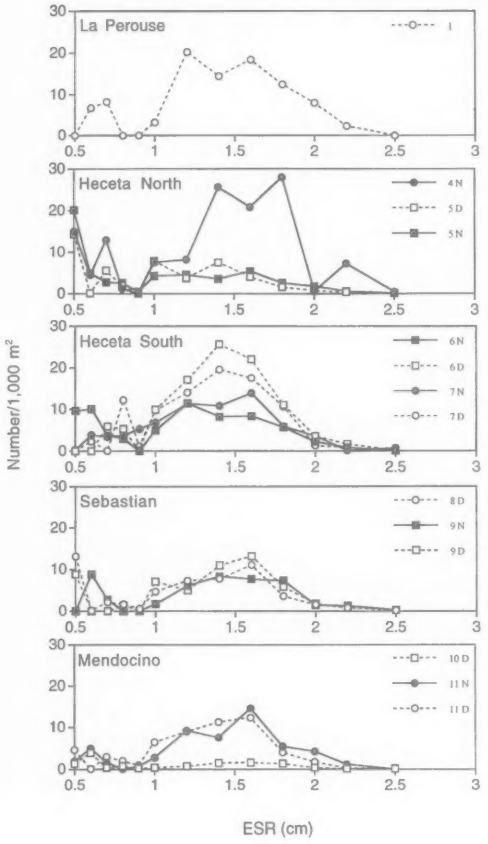

Figure 8

The equivalent spherical radius (ESR) of swimbladders for the NRL stations.

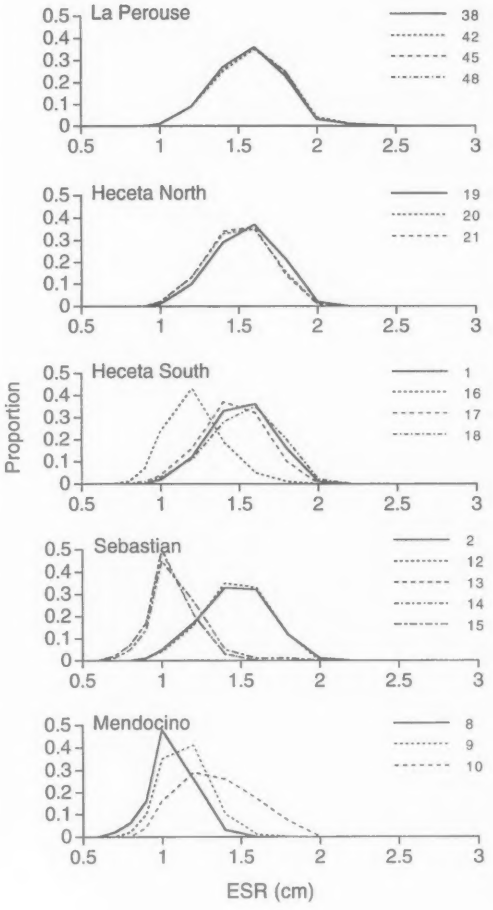

Figure 9

The equivalent spherical radius (ESR) calculated from the length of hake obtained from NMFS midwater trawls. Numbers indicate trawl number.

Discrepancies exist between the NMFS trawl estimates of hake size and our acoustic estimates at stations in the south of the study area. Only the larger size class of hake was detected acoustically whereas both large and small size classes of hake were caught in the trawls. Several explanations are suggested.

One possibility is that large hake mask the scattering from small hake. However, if ratios of small to large hake are anywhere close to those seen in the Sebastian and Mendocino trawls (Fig. 2), our inverse solution of the acoustic data would easily have detected both size classes.

Another possibility is that a physiological phenomenon caused the observed absence of a north–south trend in swimbladder size even though the southern fish were smaller. Such a phenomenon would have to cause the swimbladder-volume-to-body-volume ratio to increase in smaller hake. Differences in stomach fullness could cause such a trend. Food evacuation times are different for different food types: large hake eat fish that are evacuated slowly, small hake eat crustaceans that are evacuated quickly (Durbin et al., 1980, *in* Livingston, 1983) In addition, hake swimbladders could regress slightly in the larger fish. Although these hypotheses are possible, they would need to result in a complete cancellation of the north–south trend in fish size. This result is unlikely.

Table 2

Volume reverberation estimates of the density and depths of occurrence of probable fish swimbladders at stations along the Washington–California coast. Numbers in parentheses following densities in the 0.25 to 0.7 cm radius category are the smallest radii included in the estimates. ind. = individuals.

	Day			Night		
Station no.	Depth (m) Peak	Depth (m) Range	Density (ind./1,000 m^2)	Depth (m) Peak	Depth (m) Range	Density (ind./1,000 m^2)
0.25–0.7 cm radius						
1	200	125–450	162 (0.35)	—	—	—
4	—	—	—	70	50–550	4,855 (0.25)
5	380	250–525	21 (0.45)	70	50–550	7,974 (0.25)
6	225	125–475	30 (0.4)	<50	100–525	393 (0.3)
7	n/a	175–450	6 (0.4)	75	50–500	1,440 (0.25)
8	325	150–550	17 (0.4)	—	—	—
9	400	200–600	10 (0.45)	75	50–550	1,695 (0.25)
10	325	150–550	6 (0.45)	—	—	—
11	300	100–600	14 (0.4)	175	125–500	648 (0.3)
0.8–2.5 cm radius						
1	200	125–450	79	—	—	—
4	—	—	—	245	100–550	99
5	380	250–525	28	375	50–550	25
6	225	125–475	96	200	100–525	45
7	220	175–450	87	300	50–500	62
8	350	150–550	39	—	—	—
9	400	200–600	46	425	100–550	34
10	450	375–550	7	—	—	—
11	325	100–600	48	275	125–500	46

More likely possibilities are biogeographic effects of species composition and fish size. One possibility is that the NRL measurements were not on hake but another fish such as jack mackerel or chub mackerel, which may not have exhibited a north–south trend in fish size. However, the predominant fish in the area sampled were hake. Trawls close to the NRL stations contained only 1% jack and chub mackerel.[4] Another possibility is that large hake migrated southward with the NRL survey. This is also unlikely. The NRL survey took place in the last two weeks of August. At about the same time (17 Aug) NMFS was still collecting large hake in trawls near 51°30'N (Queen Charlotte Sound). Furthermore, the commercial fishery caught large hake off Washington as late as September and October (Dorn et al., 1994).

Table 3

Surface density estimates (kg/ha) of Pacific hake as determined by NMFS acoustic-midwater trawl survey and NRL measurements (day only). Data are grouped by NMFS geographic regions. Numbers in parentheses indicate the number of stations included in the averages for the NRL stations.

	Bottom depth (m)		
Region	NMFS 1,000–1,200	NRL inshore 900–1,500 m	NRL offshore 2,400–3,100
Canada South	91	439 (1)	—
Southern Columbia	369	348 (1)	270 (2)
Eureka	238	195 (2)	300 (2)

The most reasonable hypothesis to explain the discrepancy between trawl and acoustic estimates in hake size in the south of the study area is that the same cohort of hake was encountered at all NRL sta-

[4] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

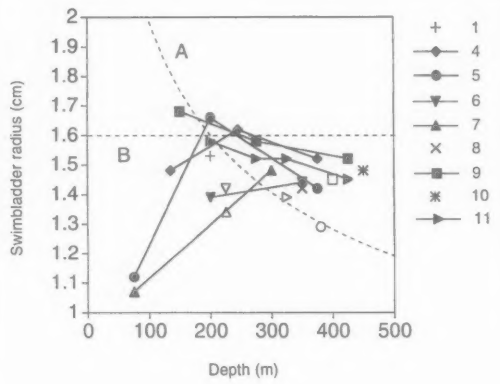

Figure 10

Mean equivalent spherical radius (ESR) in sublayers at night (dark symbols) and daytime (open symbols with same shape) for NRL stations. Stations 1, 8 , and 10 are daytime only. Dashed lines are (**A**) the calculated ESR for a swimbladder exhibiting constant mass of gas (decreases over depth), and (**B**) constant volume of gas (level with depth).

tions. There is some evidence that different cohorts stay together and remain separate from other size classes along the same section of coast. In the NMFS trawl data, most trawls show two predominant size groups, large hake (modal size >40 cm) and small hake (modal size <40 cm). These two groups rarely occurred in the same trawls. Where the two size groups overlapped (between 38°N and 43.5°N), two trawls caught large numbers of both size groups, two trawls caught large fish, and six trawls caught small fish. Some of the trawls with small fish were made near NRL stations 7 and 8. We hypothesize that at the time of the NRL survey (35 to 39 days after the NMFS survey), these small hake may have moved slightly inshore or south of the NRL stations and were replaced by larger fish.

Our interpretation of resonance and calculation of swimbladder size and fish size required assumptions of the relation of swimbladder radius, r, to fish length, L. We also assumed that this relation was constant with depth. As gadoids migrate they do adjust the gas volume of the swimbladder (Sand and Hawkins, 1973). Unfortunately our examination of swimbladder behavior in hake is inconclusive. The results of examining radius as a function of depth suggest that hake do compensate somewhat for pressure changes by adding and removing gas; however, they do not appear to compensate completely. We caution that this conclusion is conjectural and could be an artifact of size-dependent stratification of hake in the water column. Overall, bias introduced in our estimates by not accounting for the possible addition and removal of gas to the swimbladders of fish descending and ascending could have resulted in, assuming the worst case, an underestimate of length and biomass by 10% and 35%, respectively. This bias would not have affected our estimates of fish numbers because they were dependent on the number of radii independent of associated fish size.

Comparison of the NMFS survey estimates of surface density with the NRL estimates of surface density produced several important findings. First, although there were spatial and temporal differences in the surveys and although different acoustic techniques were used, the similarities between the surveys were encouraging and suggest that good accuracy is obtained with both techniques. Second, an NRL measurement at one station (one-mile drift) may be influenced by local minima or maxima in hake density. This hypothesis is suggested by the high values at station 1 where only a few days previously, in NMFS samples, much lower values were obtained. By chance at station 1, NRL may have made a measurement over an isolated concentration of fish. Third, relatively high densities of fish were seen at offshore stations in NRL sampling. Some NMFS acoustic transects suggest a high abundance of fish near the offshore limit of several transects taken near 43°N (Dorn et al., 1994). This high abundance would indicate that, at times, high densities of hake occur offshore, probably as a result of a particular set of as-yet-unknown oceanographic conditions.

This study has two important implications for fisheries surveys. First, hake may occur in high numbers, up to 300 kg/ha, approximately 50 km offshore of the outer edge of traditional fisheries acoustic surveys. Second, at these offshore sites the peak in the main scattering layer of hake may at times occur at depths of 400 to 450 m. At these depths hake could be difficult to assess by conventional 38-kHz fisheries sonars; therefore underestimates of the abundance of hake over deep water are possible.

Acknowledgments

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Abstract.—Annual fluctuation in the number of newly settled juveniles and in the stock size of the sunray surf clam, *Mactra chinensis*, were examined from 1987 to 1994 off the coast of Tomakomai, southwest Hokkaido. Stock size was estimated with a model based on two known population parameters, juvenile density and age composition. Juvenile density and the stock size (or mass) ranges were 1.3 to 157.0 ind./m^2 and 249.8 to 1,127.4 metric tons, respectively; a time lag between the relative fluctuations of both agreed with age-at-recruitment to the stock. Our results suggest that population dynamics are directly influenced by the number of juveniles. The predicted stock size approximated the measured value and, consequently, a long-term prediction of stock size was deemed possible, provided age composition and juvenile density are determined.

Population dynamics and stock size prediction for the sunray surfclam, *Mactra chinensis*, at Tomakomai, southwest Hokkaido, Japan

Izumi Sakurai
Hokkaido Central Fisheries Experimental Station
238, Hamanaka, Yoichi, Hokkaido 046, Japan
E-mail address: kb6i-skri@asahi-net.or.jp

Takashi Horii
Muroran Branch, Hakodate Fisheries Experimental Station
1-133-31, Funami, Muroran, Hokkaido 051, Japan

Osamu Murakami
Hokkaido Abashiri Fisheries Experimental Station
31, Masuura, Abashiri, Hokkaido 099-31, Japan

Shigeru Nakao
Faculty of Fisheries, Hokkaido University
3-1-1, Minato, Hakodate, Hokkaido 041, Japan

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Fishery Bulletin 96:344–351 (1998).

The sunray surfclam, *Mactra chinensis*, is a commercially important bivalve belonging to the family Mactridae and is widely distributed on the upper subtidal sandy bottom off the coast of Japan, China, Korea, Sakhalin, and the maritime province of Siberia (Habe, 1977). This clam has been harvested from marine waters off Hokkaido as incidental catch in the fishery for Japanese surfclam, *Pseudocardium sachalinensis*, which is the most commercially important bivalve in northern Japan (Kinoshita and Terai, 1954).

Recently, the demand for *M. chinensis* caught off Hokkaido has increased owing to decreasing catches on Honshu Island (Kurata, 1991). However, from 1985 to 1994, the annual Hokkaido catch fluctuated between 705 and 1,310 metric tons. In response to this wide fluctuation, stock management plans are now required. Although there are some studies of the breeding season (Miyazaki, 1957; Tomita, 1974), growth (Hanaoka and Shimazu, 1949), spatial distribution (Hayashi et al., 1965, 1967), increase in the number of juveniles (Inoue and Ozu, 1960; Yoshimatsu, 1977), and catch fluctuation (Saito et al., 1982), these studies have provided only fragmentary information. Of necessity, several temporary stock management measures, similar to those used for *P. sachalinensis*, have been implemented by several fisheries cooperative associations in Hokkaido to regulate the fishery for *M. chinensis* . These measures include limiting allowable catch and imposing a minimum harvestable shell length and period or area for fishing. We have systematically studied the life history of *M. chinensis* and have already reported on its reproductive cycle (Sakurai et al., 1992), age at first maturation (Sakurai et al., 1992), relation between

age and growth (Sakurai, 1993), spatial distribution pattern (Sakurai, 1994), and annual mortality rate (Sakurai, 1996) off the coast of Tomakomai, southwest Hokkaido, Japan.

The aim of this study is first to examine the fluctuation in density of newly settled and harvestable-size *M. chinensis* at Tomakomai and to predict the stock size according to the population parameters that we have already reported.

Materials and methods

Study area

The study was conducted on a subtidal sandy bottom off Tomakomai (42°36'N, 141°32'E), where *M. chinensis* with shells longer than 60 mm are harvested commercially. Figure 1 shows the survey area in relation to the entire fishing ground, which is about 32 km^2 in area. The survey area is situated on the fishing grounds within 6 km of shore and covers depth ranges from 3 to 11 m. The sediment in the area is fine or very fine sand with low organic carbon content, less than 0.3% of dry weight (Sakurai et al., 1991). The bottom water temperature at 10-m depth ranges between 3.0°C in March and 20.2°C in September (Sakurai, 1993).

Sampling and processing of clams

The breeding season of *M. chinensis* occurs between July and September at Tomakomai (Sakurai et al., 1992), the planktonic larval period lasts for 14–21 days (Tsurui, 1980; Kobayashi and Ujima, 1983), and shells of newly settled juveniles grow to 1–3 mm long between September and November (Sakurai, 1994). The density of newly settled juveniles was therefore

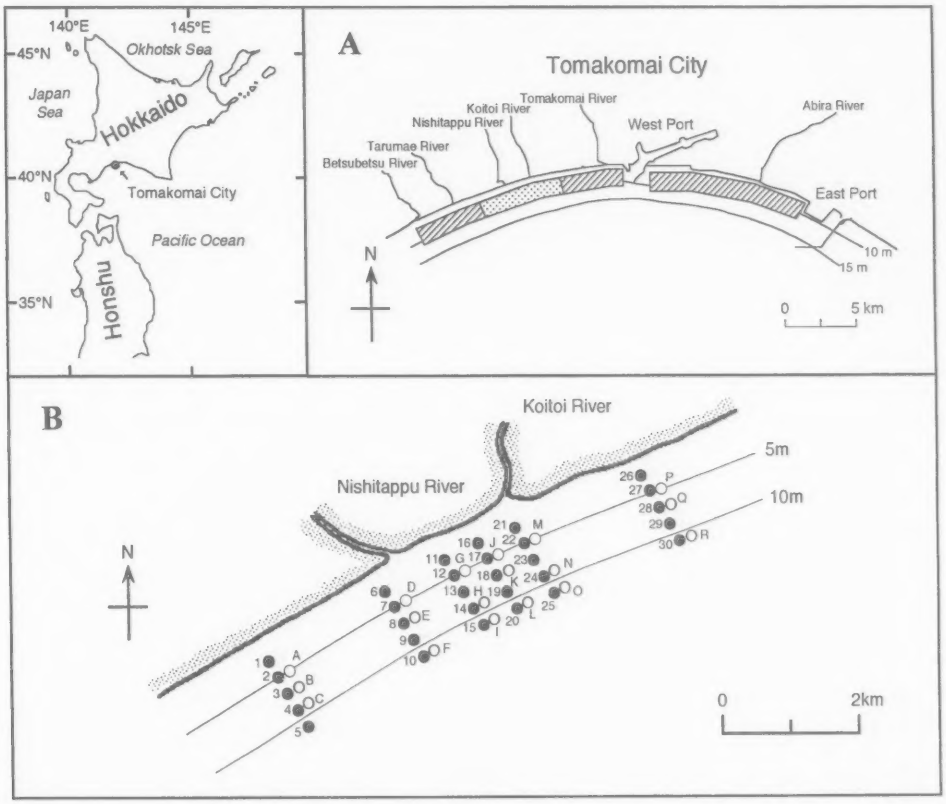

Figure 1

Location of the survey area off the coast of Tomakomai, southwest Hokkaido, Japan. (**A**) Shaded and dotted portions represent the entire fishing ground of *M. Chinensis*; dotted portion represents the survey area. (**B**) Solid and open circles indicate stations sampled by a Smith-McIntyre grab sampler and Japanese surfclam hydraulic jet dredge, respectively.

investigated during September and November in 1987–94 as tabulated in Table 1. Thirty sampling stations used for the collection of juveniles were arranged as shown in Figure 1. Each of the stations was set up at six transects including depths of 3, 5, 7, 9, and 11 m for evaluating the average density of juveniles in the fishing ground. The distribution of juveniles had been previously observed at 9 m, parallel to the shoreline in Tomakomai (Sakurai, 1994). Two samples were collected at each station with a Smith-McIntyre grab (sampling area: 0.05 m^2), sieved through a 1-mm mesh, and preserved immediately in 5% buffered formalin in the field. Sorting, identification based on morphological characteristic of the shell (Habe, 1977), and counting of juveniles were done in the laboratory.

Harvestable-size clams with shells >60 mm long were collected at 18 sampling stations in April, 1987–94 (Fig. 1; Table 1). Samples were collected with a hydraulic jet dredge (width=1.2 m, mesh size of net bag=70 mm, spacing of teeth=36 mm, and angle of tooth=60°) normally used for collecting *P. sachalinensis*. The dredge was towed parallel to shore for 50–100 m at each station. Distance of each tow was estimated by measuring the length of the dredge-connected rope wrapped by a winch. Sorting was conducted in the field. Shell lengths were measured to the nearest 0.1 mm with a sliding caliper in the laboratory. Clams with shells >60 mm long were grouped into 5-mm intervals and counted at each station. These counts were subsequently adjusted on the basis of catch efficiencies of the dredge for the different 5-mm-long intervals (60–65 mm to 0.75, 65–70 mm to 0.82, 70–75 mm to 0.88, 75–80 mm to 0.95, and >80 mm to 1.00), which were based on the selectivity curve of *M. chinensis* (Nashimoto, 1984), before density (ind./sample area) was estimated. The density was then converted to biomass (g/sample area) by using the weight (g) equivalent for the median shell length of each size interval. The length-weight equivalent was determined from 107 clams with shells 57.8–83.4 mm long sampled at station N (Fig. 1) in April 1991 as follows:

$$\log W = 3.16 \log L - 4.071, \quad (r = 0.9728, P < 0.01) \quad (1)$$

where W = the weight (g); and
L = the shell length (mm).

Next, the stock size (N_e; unit: t [age in years]) in the survey area was estimated with the following equation:

$$N_e = 18^{-1} A \sum_{i=1}^{18} b_i l_i^{-1} w^{-1} \times 10^{-6} \quad (2)$$

where A = survey area (72 × 105 m^2);
b_i = biomass (g/sample area) at each station;
l_i = tow distance (m) at each station; and
w = width of the dredge (1.2 m).

In *M. chinensis*, an external growth ring with a light penetrable band, as shown in Figure 2, is formed annually on the shell during declining water temperature, November–January, and is able to be distinguished from other rings (Sakurai, 1993). For the stock size prediction, therefore, the age of clams was determined by counting these rings. Clams with shells >60 mm long sampled at station N (Fig. 1) in April 1991 were used for age determination because the distribution of harvestable-size *M. chinensis* was observed at 9 m parallel to the shoreline in Tomakomai (Sakurai, 1996) and because specimens were considered typical of age composition in the survey area. Age determination was conducted by first washing out the shell periostracum of the specimens with a chlorine bleaching agent and by drying it in the shade. Next, the specimens were put on a light box, and external growth rings with light penetrable bands were counted.

Age-determined clams were grouped into 5-mm intervals at each age and counted. These counts (ind./sample area) were adjusted by using the above efficiencies, and then density (ind./m^2) was estimated at each age by multiplying the counts by tow distance and width of the dredge.

Table 1

Sampling dates of newly settled juveniles and harvestable-size clams of *M. chinensis*.

Year	Newly settled juveniles	Harvest-size clams
1987	20 Nov	2–5 Apr
1988	15 Nov	1–4 Apr
1989	21 Nov	2–5 Apr
1990	4 Sep	11, 12 Apr
1991	26 Nov	10, 11 Apr
1992	15 Oct	16, 18 Apr
1993	20 Sep	12, 13 Apr
1994	29 Nov	20, 21 Apr

Stock size prediction

The predicted stock size (N_{pi}; i=1992,1993, . . . , 1997; unit: t), based on the age composition in April 1991, was estimated for each year class as follows:

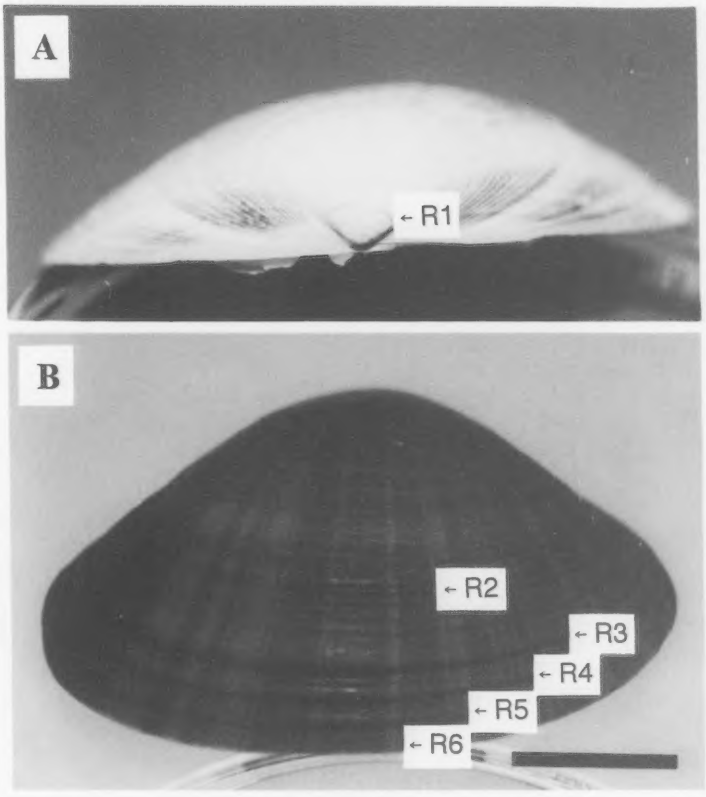

Figure 2

Mactra chinensis. Dorsal view (**A**) and outside view (**B**) of the right valve of a clam from Tomakomai in June 1992. R_n (n=1–6) indicates the nth external growth ring with a light penetrable band as clear rings could be distinguished from other innumerable fine rings. Scale bars represent 20 mm length.

$$N_{pi} = A\left\{\sum_{t=tc}^{t_{\lambda-1}} n_{t,i-1} S_t W_{t+1} + n_{0,i-3} S_{0-tc} W_{tc}\right\} \times 10^{-6} \quad (3)$$

where n_t = density (ind./m^2) at age t;
$t_{c,}$ = age at first capture; and
t_λ = longevity.

Although *M. chinensis* attains a commercial size at age 2.3 yr (i.e. in November of the second year) at Tomakomai (Sakurai, 1993), we assumed t_c to be 2.7 yr (i.e. in April of the second year) because the real stock size and the age composition in this study were investigated during April. S_t represents the survival rate at age t and was calculated from the following equation:

$$S_t = 1 - 100^{-1} m_t, \quad (4)$$

where m_t is the annual mortality rate at age t (age 0 yr: 94.0%; 1 yr: 53.1%; 2 yr: 44.8%; 3–9 yr: 42.7%) calculated with data from Sakurai (1996) with the assumption that annual mortality is constant. In April 1992–97, n_t was estimated in turn by multiplying the previous year by each S_t and by adding density of recruitment which was estimated by multiplying each $n_{0,i-3}$ by S_{0-tc}. Density at age 10 yr and older ($n_t \geq 10$) was not considered in the estimated age composition because the longevity (t_λ) of *M. chinensis* is 10 yr (Sakurai, 1993). The weight at age [t+0.7] yr, W_t, was calculated according to Equation 1 and the following equation from Sakurai (1993) :

$$L = 78.31\left\{1 - e^{-0.67(t-0.34)}\right\}, \quad (5)$$

where L = shell length (mm); and
t = age (years) of *M. chinensis*.

Results

The densities of newly settled juveniles, as shown in Figure 3, ranged from 1.3 to 157.0 ind./m^2 in 1987–94. The densities and the measured stock size of harvestable-size clams ranged from 0.7 to 3.1 ind./m^2 and from 249.8 to 1127.4 tons in 1987–94, respectively (Fig. 4).

The age composition of sunray surfclam in April 1991 is shown in Figure 5. The 2-year age group predominated with a share of 33.9%; the 6-, 7- and 3-year groups accounted for 17.3%, 12.2%, and 11.1%, respectively, and the other age groups represented less than 10% of the whole composition. Clams older than 9 years were not found in the survey area. The predicted stock size at each age in April 1992–97 calculated from Equation 3 is shown in Figure 6. It was predicted that the age groups spawned in 1988 and 1991 would predominate from age 2 to 5 in the harvestable-size clams.

Although bivalve fishing was prohibited in 1985–91 at depths of 5 to 10 m off the coast of Tomakomai, including the survey area, in order to protect *P. sachalinensis* juveniles, fishing resumed there in July 1992. Therefore, the catch of *M. chinensis* from 1992 to 1994 in the survey area was estimated by multiplying the annual catch at Tomakomai (Hokkaido, 1994, 1995, 1996) by the ratio of the survey area to the whole fishery area (Table 2). Subsequently, stock size was estimated by subtracting the value of the survey area in Table 2 from the sum of the age composition in Figure 6. The results are shown in Figure 7 together with the real stock sizes from Figure 4. The predicted values were within about 10% of the real values (Table 3).

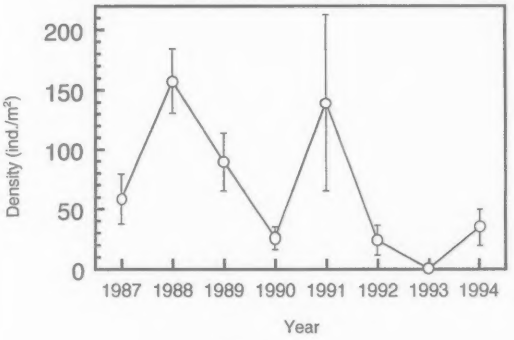

Figure 3

Annual fluctuation of the mean density of newly settled juvenile sunray surfclams. Vertical bars represent standard deviations.

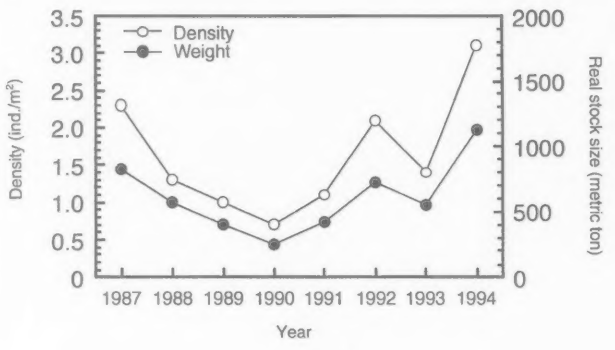

Figure 4

Annual fluctuation of the density (open circles) and the measured stock size (solid circles) of sunray surfclams.

Discussion

It is well known that marine invertebrates with planktonic larval stages show considerable fluctuations in numbers of recruits; sudden increases in numbers of juveniles occur occasionally (Hanaoka, 1972). Nakaoka (1993) noted that it is necessary for these populations to experience such sudden increases in order to maintain their populations. Sudden increases of *M. chinensis* have been reported from many of the fishing grounds in Japan. For example, a maximum density of about 980 ind./m^2 for clams with 60-mm-long shells was reported off the coast of Miura, Kanagawa Prefecture (Inoue and Ozu, 1960). In the present study, densities of newly settled juveniles ranged from 1.3 to 157.0 ind/m^2 (Fig. 3); during our study we did not find such a remarkable fluctuation in recruitment off the coast of Tomakomai compared with that observed for the population off Miura. Additionally, there were no dominant or vacant age groups in the age composition (Fig. 5); thus, it appears that the population of *M. chinensis* is maintained by comparatively stable recruitment occurring off the coast of Tomakomai.

Mactra chinensis grows to harvestable size at age 2.3 yr at Tomakomai (Sakurai, 1993); consequently newly settled juveniles spawned in the years 1987 through 1991 are presumed to have recruited to the

stock in April 1990–94. As Figures 3 and 4 show, juvenile densities in 1988, 1989, and 1991 were relatively high, causing the real stock sizes in 1991, 1992, and 1994 to increase in comparison with each previous year. In contrast, the lower juvenile densities in 1987 and 1990 caused the real stock size in 1990 and 1993 to decrease in comparison with each previous year. Therefore, it is suggested that the population dynamics at Tomakomai are directly influenced by the number of newly settled juveniles. The number of juveniles is determined by the settlement and mortality of early benthic stages (Günther, 1992). We think that it is necessary to examine the factors that cause fluctuations in the number of juveniles to gain a full understanding of the population dynamics of *M. chinensis*.

In the present study, we define a model using two known population parameters, juvenile density and age compositions, to predict the stock size of *M. chinensis*. It has been shown that the age groups that have relatively higher densities at the juvenile stage predominate for four years from age 2 to 5 in harvestable-size clams. Saito et al. (1982) reported that a large catch of *M. chinensis* continued for a few years off the coast of Ishikari, Hokkaido, because the dominant age group was maintained. This was the case in our study. Therefore, we consider that our model is appropriate for predicting the population dynamics of *M. chinensis* at Tomakomai and other sites. Furthermore, the predicted stock size of our model was close to the measured value (Fig. 7), and consequently accurate long-term prediction of stock size is possible with this model, provided age composition and juvenile density are determined.

On the other hand, analysis of age and growth based on external growth rings has been conducted for various bivalves including *Placopecten magellanicus* (e.g. Stevenson and Dickie, 1954; Claereboudt and Himmelman, 1996), *Pecten maximus* (e.g. Dillon and Clark, 1980), *Megangulus venulosus* (Goshima et al., 1991), *Mesodesma mactroides* (Defeo et al., 1992), *Clinocardium californiense* (Goshima and Noda, 1992), and *Abra tenuis* (Dekker and Beukema, 1993). However, it is suggested that age determination based on external growth rings of bivalves would be unreliable because it is difficult to distinguish the growth rings from other rings owing to several stimuli (Dillon and Clark, 1980). Nevertheless, the growth rings of *M. chinensis* have been distinguished clearly from other innumerable fine rings by checking the rings with light penetrable bands (Sakurai, 1993). These bands are regarded as nacreous layers. Therefore, age determination in the present study would be as reliable as that based on microgrowth analysis with acetate peels or thin sections (Lutz and Rhoads, 1980), and we consider that our model would be able to predict the stock size without over- or underestimates. In our model, however, annual mortality is assumed to be constant; therefore, age com-

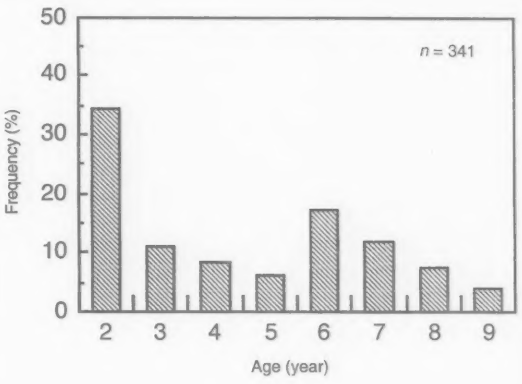

Figure 5

Age composition of the harvestable-size sunray surfclams sampled at station N (Fig. 1) in April 1991.

Table 2

Estimated catch of *M. chinensis* in the survey area and whole fishery ground off the coast of Tomakomai.

Year	Catch (metric ton)	
	Survey area	Whole fishery ground[1]
1992	7.2	36.0
1993	14.6	73.0
1994	22.0	108.0

[1] Based on data from Hokkaido Fisheries Statistics in 1994, 1995, and 1996.

Table 3

Comparison of the real (R) and predictive (P) stock size for *M. chinensis*.

Year	R (metric ton)	P (metric ton)	$(R-P) \times 100/R$ (%)
1992	728.3	651.8	10.5
1993	550.3	586.0	–6.5
1994	1,127.4	1,015.8	9.9

position would need to be reinvestigated if there was an unexpected change in mortality, such as that resulting from clams being washed ashore by a large typhoon or other storms (Sakurai et al., 1996).

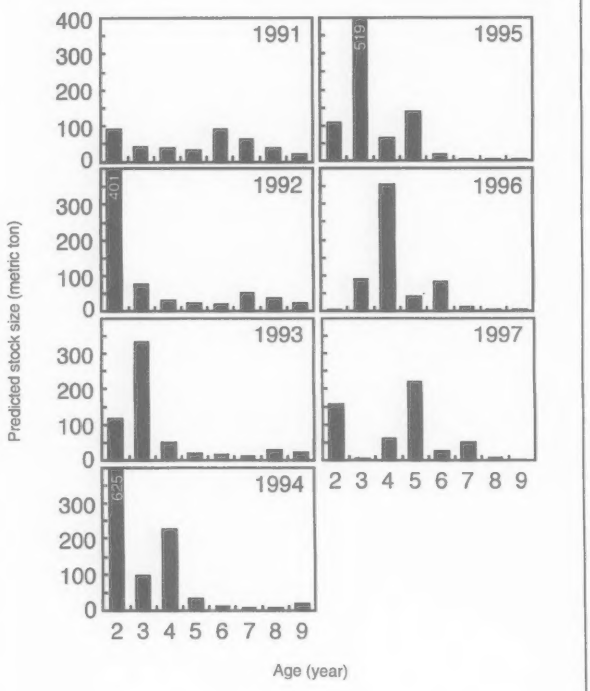

Figure 6

Predicted age compositions for the harvestable-size sunray surfclams in April from 1991 to 1997.

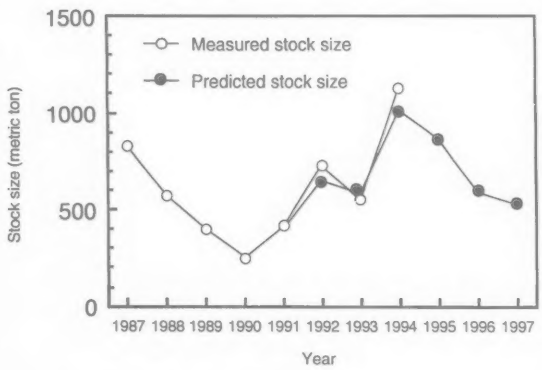

Figure 7

Annual fluctuation of the measured (open circles) and predicted (solid circles) stock size of sunray surfclams.

Acknowledgments

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Reproductive biology, growth, and natural mortality of Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911)

Andreas T. Beckmann

Prof. Hofmann Laboratory
Department of Zoology and Parasitology
Ruhr-University Bochum, ND 05-334, 44801 Bochum, Germany

Donald R. Gunderson

Bruce S. Miller

School of Fisheries
University of Washington, Seattle, Washington 98195
E-mail address (for Donald R. Gunderson, contact author): dgun@fish.washington.edu

Raymond M. Buckley

Washington Department of Fish and Wildlife
University of Washington, Seattle, Washington 98195

Betty Goetz

Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sandpoint Way N.E., Seattle, Washington 98115

In spite of being one of the most common rockfish in the rocky nearshore region of the Strait of Georgia, relatively little is known about the early life history, ecology, recruitment, and reproductive biology of Puget Sound rockfish, *Sebastes emphaeus*.

In rockfish, fecundity at 50% maturity ranges from 2,000 (*S. dalli*) to 417,000 (*S. paucispinis*) eggs per female (Haldorson and Love, 1991). Parental care in this genus is essentially lecithotrophic, characterized by primitive, unspecialized viviparity at an evolutionary stage when eggs, embryos, and early larval stages are protected inside the female body rather than born live as fairly advanced young (Wourms, 1991). Although most other northeastern Pacific *Sebastes* release their young between January and July (Westrheim, 1975), parturition occurs in August and September for Puget Sound rockfish (Moulton, 1975; Beckmann, 1995).

The goals of this study were to delineate the spawning season more closely and to determine the age and length at first maturity, the growth and mortality rates, and the length-fecundity relationship for Puget Sound rockfish.

Materials and methods

A total of 362 Puget Sound rockfish older than age 0 were collected during 23 sampling trips in coastal waters of the San Juan Islands, from 26 June 1994 to 12 March 1995 (Table 1). The fish were collected either by anglers using hook-and-line gear or by SCUBA divers using spears and hand nets. The average collection depth for these rockfish was 15 m to 21 m, with a maximum depth of 76 m.

In addition, 19 collection trips were made with hand nets for young-of-the-year (YOY) specimens. These trips extended from 26 February through 18 August 1994, and 424 YOY were obtained.

The spawning period was defined as occurring from the time when the first females with spent ovaries were caught to the time when no females with embryos were observed. A total of 253 females older than age 0, collected between June 1994 and March 1995, were classified by maturity stage according to the criteria described in Finckh McDermott (1994). Nonlinear least square regression was used to fit the data to the logistic model:

$$P_L = \frac{1}{1+e^{-(\alpha+\beta L)}},$$

where P_L = proportion mature at length L (mm FL);
α, β = constants; and
$-\frac{\alpha}{\beta}$ = length at which 50% of fish are mature ($=L_{0.5}$).

Sagittal otoliths were removed from the fish and stored in 50% ethanol. Readings prepared by the break-and-burn method were taken either from left or right otoliths, following the international convention of considering 1 January as the birth date. All final age determinations were made by the coauthor with extensive age-determination experience (B. Goetz), after examining the results obtained by the senior author and then examining edge type and annulus formation for the entire collection. A sample of 59 otoliths was read twice (with six months between readings) and showed 66% agreement (to the ex-

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Table 1

Date and sampling method for collections of Puget Sound rockfish older than age 0.

Date	Number collected	Method	Date	Number collected	Method
26 Jun 1994	6	spear	3 Aug 1994	41	hook and line
28 Jun 1994	4	spear	8 Aug 1994	19	hook and line
29 Jun 1994	12	spear or hand net	21 Aug 1994	11	spear or hook and line
5 Jul 1994	5	hook and line	26 Aug 1994	8	hook and line
6 Jul 1994	22	spear	29 Aug 1994	8	hook and line
7 Jul 1994	11	spear	30 Aug 1994	10	hook and line
7 Jul 1994	20	hook and line	2 Sep 1994	21	hook and line
13 Jul 1994	35	hook and line	6 Sep 1994	7	hook and line
22 Jul 1994	15	hook and line	10 Sep 1994	13	hook and line
24 Jul 1994	3	hand net	30 Dec 1994	21	hook and line
26 Jul 1994	6	hand net	12 Mar 1995	37	hook and line
28 Jul 1994	27	hook and line			

act year) between independent readings, with no obvious bias.

Age-length relationships were estimated from the mean length at age for age groups 1–13, derived from the otolith readings. The mean length of age-0 fish was estimated from the mean length of the YOY captured with nets during February–August 1994. Lengths for YOY were originally recorded as standard length, and were converted to fork length by using the relationship for shortbelly rockfish (*S. jordani*) reported by Echeverria and Lenarz (1984). The mean age of YOY (0.7 years) was estimated by assuming that parturition occurred on 1 September. Mean length at age for age groups 1–13 was estimated from fish collected during June–December, 1994. Data were fitted to the von Bertalanffy growth model (Ricker, 1975) with nonlinear least squares regression. Male and female fish were treated separately owing to the difference in sex-specific growth rates.

Mortality was estimated from the age composition of catches (281 fish aged successfully, sexes combined) made during June–December. Because Puget Sound rockfish are not the target of any fishery, the catch curve (Ricker, 1975) was used to estimate natural mortality (M) with linear regression of log (frequency) on age. Only fish 3 years and older were used to estimate M, because it was apparent (Fig. 1) that 1- and 2-year-olds were not fully available to our sampling gear.

Fork length (FL) to the nearest millimeter and wet gonad weight (GW) and wet somatic weight (SW) to the nearest milligram were measured for all adult females. Somatic weight was defined as the weight of the fish with the stomach emptied and the gonads removed. The gonadosomatic index ($GSI = GW/SW$) was used to determine relative reproductive effort for a mature female of average size. Allometric relationships between GW-body length and SW-body length were determined by using log-log linear regression (Gunderson and Dygert, 1988). Only fully mature females in the later stages of vitellogenesis were used in estimating GSI. Histological examination of a subsample of 12 individuals, representing a broad range of lengths and relative GSI values, showed that all of them were in the migratory nucleus stage of egg development just prior to ovulation (McDermott[1]).

Fecundity was estimated by counting all nonatretic oocytes in advanced vitellogenesis with subsamples from both ovaries of 16 fish ranging from 112 to 178 mm FL. From preliminary measurements it could be seen that vitellogenetic oocytes were at least twice the size of the resting and immature primary oocytes. All oocytes with the longest axis exceeding 250 μm were counted. A gravimetric subsampling method (Nichol and Pikitch, 1994) was chosen to estimate oocyte numbers.

Because of the nonuniform distribution of oocytes and connective tissue within the ovaries, ovarian sacs and ovarian stroma were removed prior to subsampling. Thin sections of the remaining egg mass were taken from five different transects equally spaced along the longitudinal axis of each ovary. Each subsample was weighed, pipetted into a plastic grid dish, and the eggs of each subsample were counted. Final fecundity estimates were made by multiplying

[1] McDermott, S. 1995. School of Fisheries, Univ. Washington, Seattle, WA 98195. Personal commun.

the mean oocytes/mg, averaged across all subsamples, by total egg mass weight. Fecundity data were fit to an allometric relationship with log length-log fecundity linear regression (Haldorson and Love, 1991).

Results

Females with unfertilized eggs were caught from 26 June to 8 August 1994. Embryos without pigmented eyes were observed from 22 July to 29 August, and embryos with pigmented eyes from 24 July to 29 August. The first spent female was observed on 21 August, and all mature females caught from 31 August to 10 September showed spent ovaries. Only resting females were captured on 30 December. Mature females captured on 12 March 1995, were either resting or in the initial stages of vitellogenesis. Spawning occurred over a relatively short time period, with only 9 days between the time when the first spent female and the last gravid female were observed. Ovaries did not contain developing embryos and cleaving eggs at the same time, indicating that individual Puget Sound rockfish spawn only one brood per season.

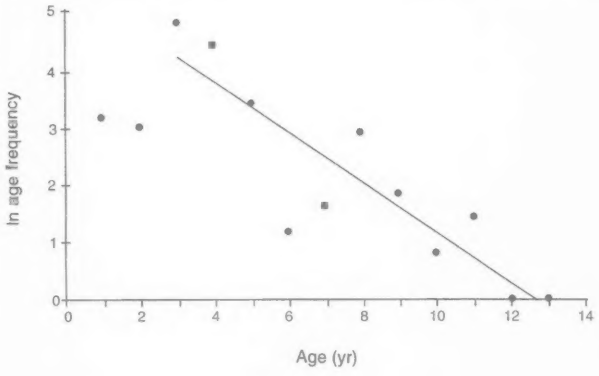

Figure 1

Estimation of natural mortality for Puget Sound rockfish (sexes combined) with a catch curve (predicted line).

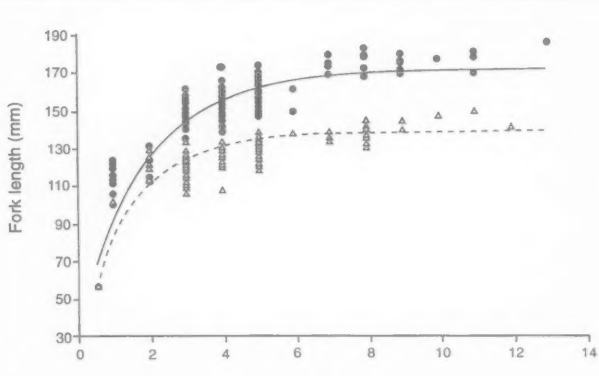

Figure 2

Comparison of female and male age-length (FL) relationships for Puget Sound rockfish. Solid line and filled circles show predicted relationship (von Bertalanffy growth model) and data for females; dashed line and open triangles show predicted relationship and data for males.

The oldest observed fish was a female 13 years old, followed by a 12-year-old male. The largest male caught was 145 mm FL and the largest female 178 mm FL (Fig. 2). The age-length relation (von Bertalanffy growth model) for male Puget Sound rockfish was $L_t = 137.39\ (1 - e^{-0.7042(t+0.3232)})$ and for females $L_t = 170.72\ (1 - e^{-0.5353\ (t+0.4603)})$. Based on the regression result of ln(frequency) = 5.554–0.44 (age), the instantaneous annual rate of natural mortality (M) for fish 3 years and older was estimated to be 0.44 (Fig. 1).

Female Puget Sound rockfish reached sexual maturity at a median length of $L_{0.5}$ = 121.71 mm *FL* (Fig. 3) corresponding to a predicted age of 1.87 years with the von Bertalanffy growth model. The length-maturity parameters derived from the logistic model were $\alpha = -39.678$ and $\beta = 0.326$. The average length of all mature females larger than $L_{0.5}$ was L_{AV} = 150.93 mm.

The somatic weight-length relationship was $SW = 5.882 \times 10^{-5}\ L^{2.687}$ with the predicted somatic weight for L_{AV} = 42.06 g. The gonad weight-length relationship was $GW = 5.869 \times 10^{-7}\ L^{3.151}$ with the predicted gonad weight for L_{AV} = 4.30 g. From these two weights the GSI for Puget Sound rockfish was computed as 0.10.

The lowest fecundity was 3,295 eggs for a female of 112 mm FL and the highest was 57,787 for an individual 156 mm FL (Fig. 4). The length-fecundity (*F*) relationship was $F = 0.052\ L^{2.679}$, and the fecundity for a mature female of average length (150.93 mm) was estimated to be 35,723 eggs. The estimated fecundity per gram for a female $L_{0.5}$ cm long (Haldorson and Love, 1991) was 779 eggs.

Although egg size was variable, the majority of the eggs within an individual female were about the same size and at the same developmental stage. The time span between the capture of the first fertilized female and the first spent female yields a rough estimate of 30 days for the gestation period.

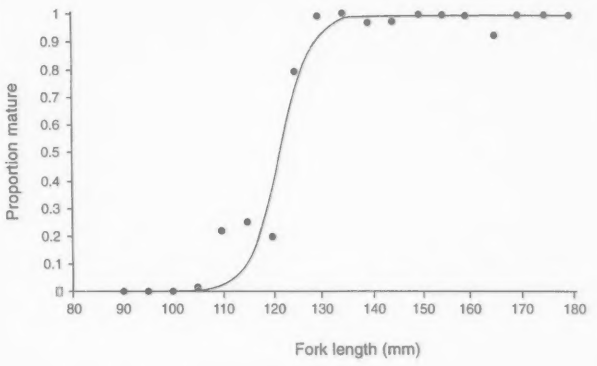

Figure 3

Length-maturity relationship predicted for female Puget Sound rockfish (predicted line). Solid circles indicate data.

Discussion

Puget Sound rockfish show high fecundity per gram, early age at maturation, small body size, and a relatively short life expectancy compared with other rockfish of the genus. No other rockfish studied to date has a higher fecundity per gram at $L_{0.5}$ (Haldorson and Love, 1991). A high natural mortality would be expected to accompany these life history characteristics, and the estimated M of 0.44 is high compared with that of other rockfish .

Puget Sound rockfish have a GSI (0.10) close to that of other early maturing rockfish (e.g. shortbelly rockfish, GSI=0.07, M=0.26, maturation age=2 years; Gunderson, 1997). However, a comparison of the catch-curve estimate of M with empirically derived estimates suggests some possibility that the catch curve is based on an unrepresentative sample and has been overestimated. The maximum age observed in our study (13 years) corresponds to an M of 0.32 with Hoenig's (1983) empirical estimation technique, whereas the GSI (0.10) gives an estimate of M = 0.18 with Gunderson's (1997) estimator.

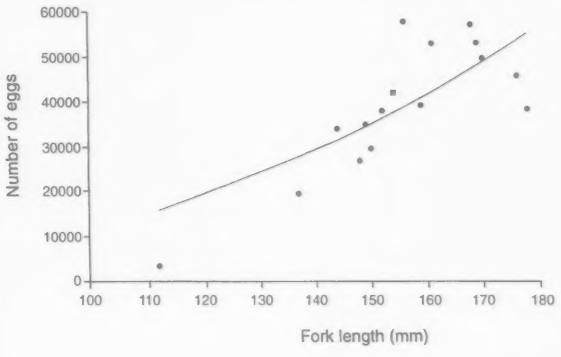

Figure 4

Length-fecundity relationship for female Puget Sound rockfish (predicted line). Solid circles indicate data.

A constant recruitment is assumed if the catch curve is used, yet the data in Figure 2 suggest that the 1988 year class (age 6 in 1994) appears to have recruited at significantly lower levels than the others. Our catch-curve estimate of M should probably be regarded as provisional, and additional collections of age-composition data or tagging studies should be undertaken to validate it.

The fecundity of 3,300–57,800 eggs observed for Puget Sound rockfish is in the range of fecundities of similar-size rockfish. Shortbelly rockfish (18–31 cm TL) has a fecundity from 7,000 to 50,000 (Hart 1973). Our fecundity estimates for Puget Sound rockfish are comparable to those obtained by Moulton (1975).

The estimated gestation period for Puget Sound rockfish is similar to the 29-day gestation period reported for yellowtail rockfish (*S. flavidus*), a species which has been shown to be lecithotrophic, providing only a negligible amount of maternal energy during gestation (Hopkins et al. 1995). The high fecundity per gram and relatively brief gestation period suggest that parental care is limited in comparison to other rockfish.

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Age, growth, and calving season of bottlenose dolphins, *Tursiops truncatus*, off coastal Texas

Stephanie Fernandez

Instituto Tecnologico y de Estudios Superiores de Monterrey
Campus Guaymas, Apdo. Postal 484, Guaymas, Sonora 85400, Mexico

Aleta A. Hohn

Office of Protected Resources
National Marine Fisheries Service, NOAA
1335 East-West Highway, Silver Spring, Maryland 20910
Present address: National Marine Fisheries Service
101 Pivers Island Road
Beaufort, North Carolina 28516

E-mail address (for A.A. Hohn, contact author): aleta.hohn@noaa.gov

Life history studies of bottlenose dolphins, *Tursiops truncatus*, in North America began over a century ago with observations by True (1890) on dolphins captured in a directed fishery along the coast of Cape Hatteras, North Carolina. He detected an approximately equal sex ratio but variability in size among individuals in almost every catch. He noted tooth development (eruption) and state of fissure of the umbilical cord in young dolphins, as well as reproductive state in females (i.e. lactating or pregnant). Furthermore, he suggested that calving took place primarily in the spring. Since then, much of the knowledge of life history of bottlenose dolphins in the western Atlantic has been obtained from dolphins captured incidentally during fishing operations or directly for research or display, and from stranded animals (Sergeant et al., 1973; Hohn, 1980; Hersh, 1987; Barros and Odell, 1990; Mead and Potter, 1990). More recent and extensive information on age, growth, and population biology has been obtained from a long-term study of free-ranging bottlenose dolphins in Sarasota Bay, Florida (e.g. Hohn et al., 1989; Scott et al., 1990; Wells and Scott, 1990; Read et al., 1993).

Equivalent life history studies have not been conducted on bottlenose dolphins from the north or western Gulf of Mexico, although this is the most common cetacean inhabiting the coastal waters of the northwestern Gulf (Barham et al., 1980; Fritts et al., 1983; Leatherwood and Reeves, 1983; Mullin et al., 1990). It also is the most commonly stranded species along the Gulf coast, particularly along the coast of Texas. Strandings of bottlenose dolphins have been recorded routinely in Texas since 1974 (Jones, 1987; Schmidly and Shane[1]). Since late 1980, the Texas Marine Mammal Stranding Network (TMMSN) has recovered over 800 carcasses. In the spring of 1990 and 1992, the TMMSN documented the highest frequency of bottlenose dolphin strandings since the program began (Hansen[2]). Unusually high mortalities among bottlenose dolphins along the Texas coast have emphasized the need for baseline information on their life history to allow better interpretation of the impacts of these mortalities on the populations. The available source of data and samples to begin such studies is the strandings themselves. This study of stranded specimens was conducted to estimate 1) age structure of stranded specimens, 2) growth from length-at-age data, 3) mean length at birth, 4) calving season, and, where possible, 5) age and length at sexual and physical maturation. These data provided the material for a preliminary examination of the life history of bottlenose dolphins that inhabit the coastal waters of Texas.

Materials and methods

From January 1981 through December 1990, 898 stranded bottlenose dolphins (373 males, 292 females, and 233 specimens of unknown sex) were recovered by members of TMMSN along the 715-km Texas coastline. Tooth sections were prepared for 205 specimens (Table 1), which comprised the entire sample of specimens from which teeth were collected. The teeth were fixed in 10% buffered formalin and processed following the decalcification, sectioning, and staining protocol described by Hohn et al. (1989). Age was estimated by counting the number of GLG's (growth layer groups, Perrin and Myrick, 1980) in dentine and cement without reference to data on the sex and length

[1] Schmidly and Shane. 1978. A biological assessment of the cetacean fauna of the Texas coast. Rep. U.S. Mar. Mamm. Comm., contract report MMC-74/05, 38 p.

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Table 1

Sample sizes and sex ratios of bottlenose dolphins, *Tursiops truncatus*, stranded along the Texas coast from January 1981 through December 1990 and of the subsample for which age was estimated.

Sample	Males	Females	Sex unknown	Sex ratio (M:F)
Total	373	292	233	1.3 : 1
Aged	78	81	36	1 : 1.04
<1.0 yr old	22	10	7	2.2 : 1
1–20 yr old	46	39	22	1.2 : 1
>20 yr old	10	32	7	1 : 3.2

of the animals. The age structure of males and females was compared by using the nonparametric Kolmogorov-Smirnov (K-S) test (Sokal and Rohlf, 1981).

Growth was determined by fitting the nonlinear, least-squares Gompertz model to length-at-age data (SAS Institute, 1985):

$$S(t) = A\left(\exp\left(-b\exp(-k)\right)\right), \quad (1)$$

where S = a measure of size (cm);
A = asymptotic length;
b = the constant of integration;
k = the rate of growth constant; and
t = age (yr) (Laird, 1966).

Total body length was measured to the nearest centimeter in a straight line from the tip of the upper jaw to the notch of the fluke (Norris, 1961). Predicted asymptotic lengths for males and females were compared by using the approximate t-test (Sokal and Rohlf, 1981). These lengths were then compared with the corresponding asymptotic lengths for male and female bottlenose dolphins from Sarasota Bay, Florida (Read et al., 1993).

Length at birth was estimated in three ways: 1) as the mean length of 21 specimens from the entire data set (n=898) determined to be neonates on the basis of the presence of remains of the umbilical cord or folded dorsal or caudal fins; 2) as the mean length of 21 specimens (no overlap with the previous sample of 21) estimated to be <0.1 year old because the neonatal line in tooth sections had not yet formed or had just started to form (Hohn and Hammond, 1985); 3) as the predicted value from the Gompertz model. Calving season was also identified in three ways: as the date of stranding of 1) neonates, 2) specimens <0.1 year old, and 3) specimens measuring 90–120 cm in length.

Reproductive data were available for 57 females from the total sample of stranded females from which some data were collected (n=292). Teeth were available for 25 of these. Sexual maturity of females was determined by noting 1) the presence or absence of a corpus of ovulation from external examination of ovaries or 2) the presence of a fetus or an extended uterus, indicating a pregnancy. Sexual maturity of males could not be evaluated because few data or samples from testes were collected.

Vertebrae from 24 males, 25 females, and 12 dolphins of unknown sex were collected. All were examined for state of physical maturity. From this sample, teeth were available for only 11 males, 12 females, and 8 specimens of unknown sex. Physical maturity was determined by noting the degree of fusion of the epiphysis to the centrum of thoracic and lumbar vertebrae. Three categories were used to classify the specimens: a) not fused (immature), b) fusing (maturing), and c) fused (mature).

Results

Age and sex composition

Estimates of age were obtained for 78 males, 81 females, and 36 specimens of unknown sex (Table 1; Fig. 1). For an additional 10 dolphins (5 males, 3 females, and 2 dolphins of unknown sex), only minimum ages, ranging between 12+ to 20+ years, were obtained because poor-quality tooth sections precluded accurate age estimates. These 10 specimens were excluded from all analyses. Occlusion of the pulp cavity was not seen in any of the tooth sections.

The oldest male and the oldest specimen of unknown sex were 33 years old and the oldest female was 41 years old (Fig. 2). Age distributions for males and females were significantly different (K-S test, P<0.01). Specimens less than 1 year old accounted for a relatively large part (20%) of the aged sample and were skewed towards males, but with increasing age, the proportion of females in the sample increased significantly (chi-square (χ^2) P=0.003, for data stratified by age group 0–0.9, 1.0–9.9, 10.0–19.9, and ≥20 years; Table 1). Because of the relatively large number of males less than one year of age, the K-S test was rerun with that age class excluded for both males and females. The difference was still significant (K-S test, P<0.01).

Growth

The Gompertz model gave predicted asymptotic lengths of 263.5 cm for males and 244.7 cm for fe-

males. Trends in the residuals, however, showed that the fit was poor for a number of age classes (Fig. 3). To obtain a better predictor, the model was fitted to a data set that excluded all specimens less than 1 year of age, analogous to the procedure in Read et al. (1993) where the Gompertz model was found to describe well the growth of bottlenose dolphins from Sarasota Bay, Florida. With this subset of data, asymptotic length was slightly higher for males (268.0 cm) and for females (246.7 cm) but neither were significantly different from the predicted values from the total sample (approximate t-test, $P>0.05$, Table 2). Trends in the residuals showed that predicted length at age was a better fit for ages 1–9 years and was slightly overestimated at asymptote.

In an attempt to find a fit with evenly dispersed residuals, the Gompertz model was modified to fix length at birth at 109.5 cm, as calculated below by independent means, rather than by solving for the asymptotic value, A:

$$S(t) = 109.5\Big(\exp\big(b\big(1-b\exp(-k)\big)\big)\Big). \qquad (2)$$

Predicted asymptotic length was 261.7 cm for males and 244.4 cm for females. Predicted length from birth through age 2 years was very similar to that estimated from the total sample with the Equation 1 version of the Gompertz model. Length at age was still underestimated and this derivation of the model did not improve the fit.

Although none of the iterations produced a fit that represented all age classes well, the best overall predicted values occurred with Equation 1) when specimens <1 year of age were excluded (Fig. 3) and, for comparative purposes, predicted lengths were taken from this model (268 cm for males and 246.7 cm for females). Males were significantly larger than females at asymptotic length (approximate t-test, $P<0.05$). Asymptotic lengths of males and females were not significantly different (approximate t-test, $P>0.05$) between dolphins from Texas and Sarasota Bay, Florida (Table 2).

Length at birth and calving seasonality

There was no difference in length at birth between male and female neonates or between males and females <0.1 year old (t-test, $P>0.05$). Therefore, data were combined to produce a single estimate with each method (Table 3). Mean length at birth from combined data was not significantly different between these two methods (t-test, $P>0.05$), therefore the total data set was combined (males, females, and sex unknown, $n=42$) to give an estimated length at birth of 109.4 cm (SD=8.5). Length at age 0 estimated from the Gompertz curve was greater than length at birth estimated from the more direct measures. In addition, because the best-fit version of the Gompertz

Figure 1

Midlongitudinal stained thin sections from the tooth of a 29-year-old, 261-cm female bottlenose dolphin, *Tursiops truncatus*, stranded in Texas. Growth layer group (GLG) boundaries were considered to be the relatively thin dark layers; most of these are easily visible. Boundaries between the first few layers are marked with a small black line on the upper left side of the section. The last few, very fine GLG's near the pulp cavity are difficult to see at this low magnification.

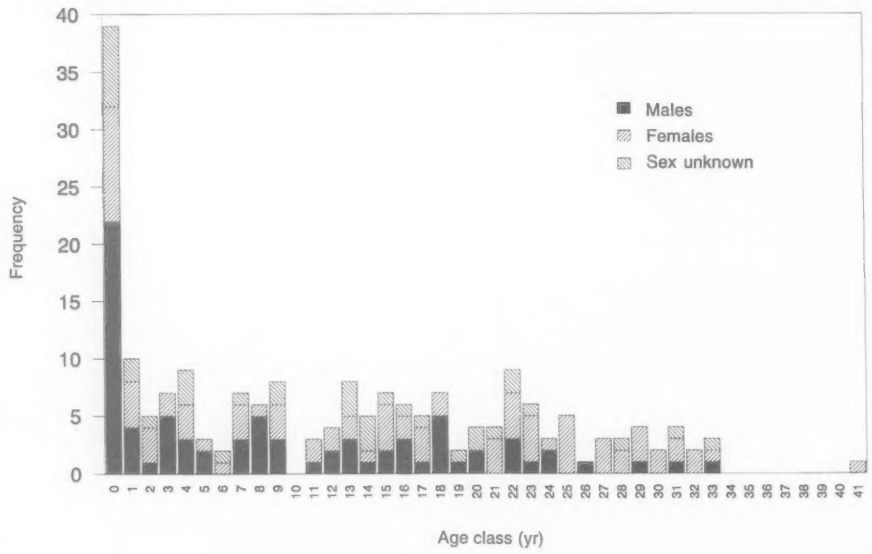

Figure 2

Age distribution of bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas from 1981 to 1990.

Table 2

Parameter values and their asymptotic standard errors (SE) from the Gompertz growth model fit to two sets of length-at-age data from bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The first set included all the available data; the second set was a subset of the first set that excluded specimens <1.0 yr of age. A = asymptotic length, b = the constant of integration, and k = the rate of growth constant. n = number of dolphins in each sample.

	n	$A \pm$ SE	$b \pm$ SE	$K \pm$ SE
Female length				
All data	78	244.7 ± 1.90	0.755 ± 0.0423	0.497 ± 0.0490
Specimens of age <1.0 yr excluded	68	246.7 ± 2.22	0.482 ± 0.0873	0.294 ± 0.0655
Male length				
All data	75	263.5 ± 2.93	0.785 ± 0.0308	0.351 ± 0.0313
Specimens of age <1.0 yr excluded	54	268.0 ± 3.64	0.592 ± 0.0679	0.234 ± 0.0388

model excluded specimens less than 1-yr-old extrapolation to age 0 to estimate length at birth was inappropriate. The ratio of mean length at birth to asymptotic length was 40.8% for males and 44.4% for females.

The mode in strandings of neonates (n=12 of 21) and specimens <0.1 year of age (n=11 of 21) occurred in March (Fig. 4). In both data sets, 86% of the specimens stranded during March and April. Except for five specimens found in November and December, all neonates stranded from February through June.

Sexual and physical maturation

Because reproductive data were collected from only 57 females (Table 4), the sample size was too small to estimate the mean age and length at sexual maturation. Only seven pregnant females were noted; the smallest was 233 cm and the longest was 335 cm. The latter, an extremely large female, also had the largest fetus (122-cm male) recorded in the TMMSN stranding database. Teeth were available for three of the seven pregnant females, and they were esti-

mated to be 9.8, 23, and 27 years of age. A 4.8-year-old pregnant female, 245 cm long, was excluded from this sample owing to possible mislabeling of samples. No reproductive data were available for males.

Mean age and length at physical maturation could not be calculated owing to the small sample sizes (Table 4). Two specimens, a 280-cm male and a 253-cm female, were notable because they were relatively large yet physically immature.

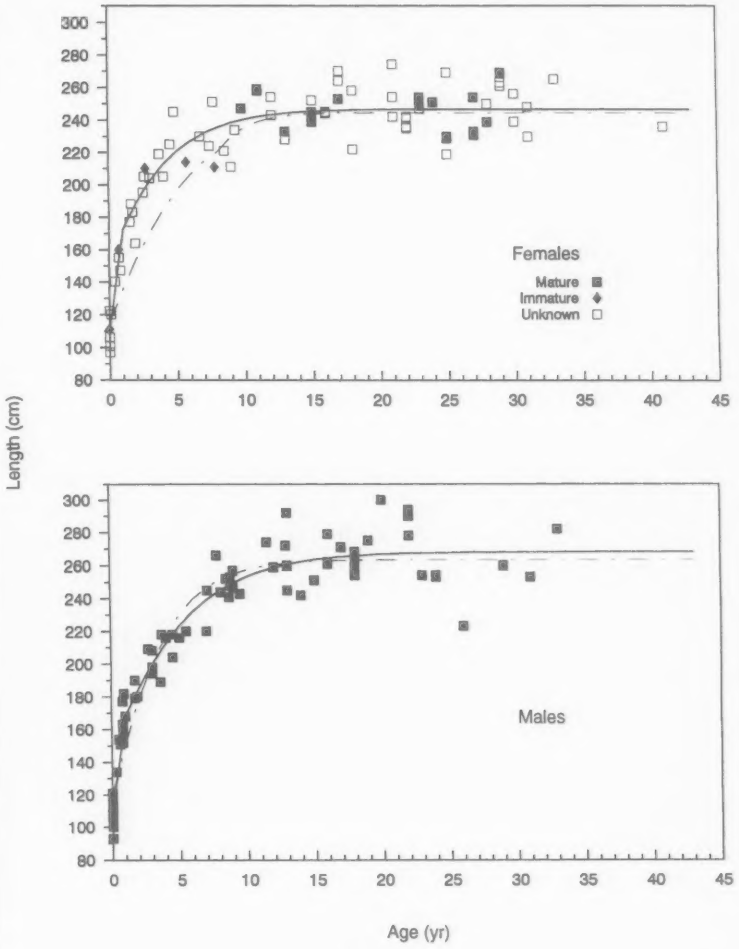

Figure 3

Scatterplots of length at age for female and male bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The solid lines represent the predicted growth trajectory from the Gompertz model when specimens less than 1 yr old are excluded; growth between birth and age 1 was determined by using the independently estimated length at birth and the predicted length at age 1. The dashed lines represent the predicted growth trajectory from the Gompertz model with the entire data set. Although the asymptotic lengths are similar, the growth trajectories are different, particularly for females.

Discussion

Despite the widespread distribution and high abundance of bottlenose dolphins along the Atlantic and Gulf of Mexico coasts of the United States, the majority of biological information for this species has come from a few locations, a relatively small number of studies, and small sample sizes. Basic questions still remain throughout much of the range. The current data provided the opportunity to begin to evaluate similarities and differences in bottlenose dolphin life history in relation to areas where previous studies had been conducted.

Results from this study support the hypothesis that in bottlenose dolphins sexual dimorphism in body length is not exhibited at birth (Sergeant et al., 1973; Hohn, 1980; Kasuya et al., 1986; Cockcroft and Ross, 1990) but does occur in adults (Read et al., 1993). Although a number of studies have concluded that sexual dimorphism in adult size does not exist in bottlenose dolphins from the Atlantic and Gulf of Mexico coasts of the United States (for example, Hohn, 1980; Hersh, 1987; Hersh et al., 1990; Mead and Potter, 1990), the contradictory results could be explained partly because sample sizes in earlier studies were small but also because these other studies did not fit a growth curve to obtain predicted asymptotic lengths that could be directly compared (Read et al., 1993). The dimorphism at asymptotic length may result from females diverting energy to reproduction at the same ages that males are gaining girth and mass (Read et al., 1993) and thus would explain why sexual dimorphism occurs in adults, but not at birth.

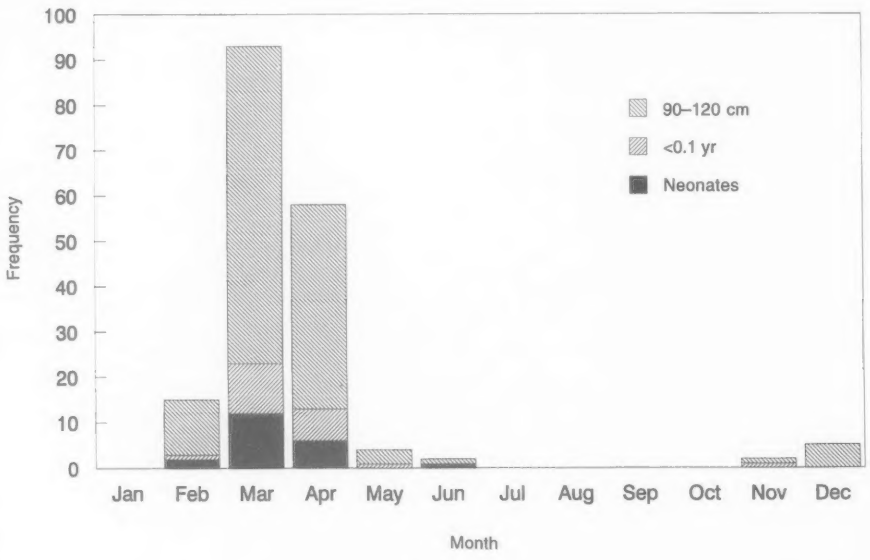

Figure 4

Calving seasonality illustrated as the monthly distribution of strandings of neonates, specimens <0.1 years old, and specimens 90–120 cm in length.

Table 3

Estimated length at birth (cm) for bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The two methods of defining a newborn animal ("neonates" and "specimens <0.1 yr") are described in the text. The Gompertz values were the predicted lengths at age 0 (L_0) from the Gompertz curve fitted to age-at-length data for males and females. The samples for neonates and specimens <0.1 yr are independent. n = number of dolphins in each sample.

	Males	Females	Sex unknown	Total
Neonates				
mean	109.5	111.2	107.3	109.5
SD	9.3	13.6	5.0	9.3
n	12	5	4	21
range	94–124	91–128	102–112	91–128
Specimens < 0.1 yr				
mean	109.7	107.4	113.7	109.7
SD	7.7	9.7	3.5	7.5
n	13	5	3	21
range	93–121	97–122	110–117	93–122
Gompertz				
mean	128.2	115.1		
SD	3.6	4.9		
n				
range				

Bottlenose dolphins from the coast of Texas are not significantly different in adult size from those in Sarasota Bay, Florida (Read et al., 1993), the only other western Atlantic or Gulf of Mexico area for which growth curves have been fitted to length-at-age data. Contrary to the analysis of Read et al. (1993), however, we found that the Gompertz curve did not adequately describe growth across all age classes. The curve did not respond readily enough to simulate rapid growth during the first couple of years. The fit was improved by excluding specimens less than 1 year of age, the phase of growth where the rate and absolute incremental increase are greatest. Although this approach provided a data set comparable in range of ages to that used in Read et al. (1993), the Gompertz model proved a better predictor for the Sarasota Bay, Florida, sample where the predicted length of young animals was larger. The large and unbiased sample of live animals that represented most of the individuals in Sarasota Bay probably accounts for these differences. The fit might be further improved if the sample was large enough to allow for a two-stage Gompertz fit (e.g. see Perrin et al., 1976) that would accommodate the growth spurt occurring at maturation (Cheal and Gales, 1992; Read et al., 1993).

Estimates of length at birth are not available for the Sarasota Bay animals. Along the mid-Atlantic

coast of the United States, however, Mead and Potter (1990) estimated length at birth (117 cm) as the mean length of 13 specimens classified as neonates on the basis of a folded or flaccid dorsal fin. Using the equivalent data set from the Texas sample (neonates), we found that the length at birth of mid-Atlantic coastal bottlenose dolphins was significantly different (t-test, P=0.02) from the estimate of 109.4 cm for Texas animals, but this result should be considered preliminary until larger sample sizes are available.

Mean length at birth may best be estimated by using morphological characteristics. Tooth-layer deposition patterns proved to be accurate in comparison to results from morphological data and can be valuable when morphological characteristics are not recorded. The method, however, is more time consuming. In contrast, use of predicted lengths of 0-yr-old animals from a fitted growth curve may be inaccurate, as was the case with this sample.

Strandings of neonates along the Texas coast are highly seasonal, with a mode in March. Using stranding data, Urian et al. (1996) found a significant difference in calving season between bottlenose dolphins from the coast of Texas (citing this data set) and those from the central-west coast of Florida, including Sarasota Bay. Stranding patterns may not accurately reflect actual calving, however, because neonates that did not survive may be those that were born earlier or later than calves that did survive. In the Sarasota Bay area, Urian et al. (1996) found that the mean date of birth estimated from stranded neonates was 16 days earlier than that estimated from sighting records of females with new calves, although this difference was not significant. They suggested that the photo-identification data may also be biased owing to unequal and discontinuous distribution of survey effort, a finding also made by Caughley and Caughley (1974). Further error may arise from lack of detection of neonates that stay very close to the female. Photo-identification studies of calving season along the Texas coast identified a peak in number of neonates in May (Shane, 1977). This later detection of neonates, in comparison with stranded animals, is consistent with the results from the central-west coast of Florida and limitations of the photo-identification method.

The increase in proportion of females with age in the Texas sample is similar to a general pattern identified in delphinids, with a slight bias towards young males and old females (Ralls et al., 1980; Perrin and Reilly, 1984; Wells and Scott, 1990). Some authors have attributed this shift to higher natural mortality rates in males (Kasuya, 1976; Miyazaki, 1977; Wells and Scott, 1990). No direct or unbiased estimates of mortality are available for bottlenose dolphins from Texas, and patterns from stranded animals may not accurately reflect the population.

Table 4

Sample sizes and descriptions of sexual and physical maturity in bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. Reproductive data were not collected for males.

Sample	Females	Males	Sex unknown
Total stranded with at least minimum data collected	292	373	233
With reproductive data	57		
Number immature	17		
Number mature	40		
Largest immature (cm)	235		
Shortest mature (cm)	225		
With reproductive and age data	25		
Number immature	6		
Number mature	19		
Oldest immature (yr)	7.8		
Youngest mature (yr)	9.8		
Youngest pregnant (yr)	9.8		
With vertebrae examined for physical maturity	25	25	12
Number immature	10	16	8
Number maturing	2	2	0
Number mature	13	7	4
Largest immature (cm)	253	280	253
Shortest mature (cm)	219	237	231
With physical maturation and age data	12	11	8
Number immature	2	7	4
Number maturing	1	1	0
Number mature	9	4	4
Oldest immature (yr)	15	16	9.9
Youngest mature (yr)	13	18	20

The proportion of specimens less than 1 year of age in the sample of stranded animals is higher than expected. In bottlenose dolphins from Sarasota Bay, Florida, Wells and Scott (1990) calculated that animals in the same age class represented 3.4% of the population, and that the crude birth rate was 5.5% annually (range of 1.1–10.4% over eight years). The higher percentage (20%) of calves in the Texas sample most likely is due to the high rate of mortality in neonates and young calves. It is also interesting to speculate that cows with young calves may occupy more protected waters and, therefore, are more likely to wash ashore when they die, contributing to a stranding sample not representative of the population.

Some of the specimens in the sample were notably large, e.g. a 300-cm male, a 335-cm female, a 280-cm

physically immature male, and a 253-cm physically immature female. Although the sample is assumed to consist predominantly of the coastal form of bottlenose dolphins, it is possible that specimens from the larger offshore form (Duffield et al., 1983; Hersh and Duffield, 1990; Hersh et al., 1990) were included. These specimens remained in the sample because they were not specifically identified as offshore individuals from independent criteria. The inclusion of offshore individuals of various lengths may be responsible for some of the variability in length at age seen in this study.

Results from this study show that bottlenose dolphins from the coast of Texas have some similarities and some differences with bottlenose dolphins from the west coast of Florida and the mid-Atlantic coast of the United States. However, samples size are small, precluding, for example, any substantial reproductive analyses. We strongly encourage the routine collection of reproductive and other samples from stranded specimens. Such basic information as the average age at sexual maturation and calving interval remains unknown even though large numbers of bottlenose dolphins are found stranded each year.

Acknowledgments

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Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina

Mariano Koen Alonso
Enrique Alberto Crespo
Néstor Aníbal García
Susana Noemí Pedraza
Mariano Alberto Coscarella

Centro Nacional Patagónico (CONICET)
Universidad Nacional de la Patagonia and Fundación Patagonia Natural
Boulevard Brown s/n, (9120) Puerto Madryn, Chubut, Argentina
E-mail address (for M. Koen. Alonso): koen@cenpat.edu.ar

The dusky dolphin, *Lagenorhynchus obscurus*, is probably the best known species of the genus *Lagenorhynchus* in the Southern Hemisphere. It is common in temperate waters of New Zealand, South Africa, Peru, northern Chile, and Argentina (Crespo, 1991; Van Waerebeek, 1992; Crespo et al., in press). Incidental catches have been recorded in coastal and offshore fisheries of Argentina (Corcuera et al., 1994; Crespo et al., 1994a, 1994b; Dans et al., in press), whereas directed captures have occurred off Peru (Read et al., 1988; Van Waerebeek and Reyes, 1990; Reyes, 1992).

The biology of dusky dolphins has been studied in Argentina since the 1970's (Würsig and Würsig, 1980; Würsig and Bastida, 1986; Dans et al., 1993). A detailed behavioral study was carried out at Península Valdés (Würsig and Würsig, 1980), and preliminary information about the reproductive biology of females was obtained by Dans et al. (1993, 1997).

Feeding habits have been briefly described for dusky dolphins from New Zealand (Gaskin, 1972), Patagonia (Dans et al., 1993; Crespo et al., 1994c), and Antarctic and sub-Antarctic waters (Goodall and Galeazzi, 1985). In Patagonia, the behavior of dusky dolphins feeding on Argentine anchovy, *Engraulis anchoita*, schools has been described by Würsig and Würsig (1980). A more recent and detailed study of their feeding habits by stomach content analysis was carried out in coastal waters of central Peru (McKinnon, 1994). The Peruvian sample consisted of animals caught mostly in gill nets (McKinnon, 1994). Peruvian anchoveta, *Engraulis ringens*, was the most important prey species for Peruvian dusky dolphins, accounting for 92.5% in number and 83.8% in weight of the total sample, and 97.8% frequency of occurrence (McKinnon, 1994). Differences in diet between lactating and nonlactating mature females were not found, and the anchoveta was almost the exclusive prey species in both sexes (McKinnon, 1994).

The objective of the present study is to describe the diet of the dusky dolphin in Patagonia in terms of both species composition and prey size. Seasonal and annual composition were not investigated because the sample size was small when subdivided along these lines.

Materials and methods

The sample consisted of 25 dolphins (6 males and 19 females) caught incidentally between November 1989 and April 1994 by the trawling fishery that operates over the Patagonian Continental Shelf. All dolphins were caught in the area between 43°S and 46°30'S and between the coastline and the 100-m isobath. Most individuals were frozen onboard to –20°C when they were caught.

The total weight, standard length, and other body measurements (Norris, 1961) were recorded for each dolphin before dissections were made. Stomach contents were collected and then stored, either frozen or in 70% alcohol. They were separated with several sieves with a mesh size between 25 mm and 0.5 mm. Flesh material from the sieved contents was placed in a deep, water-filled plastic tray, enabling removal of the remaining flesh material. Otoliths, fish bones, and cephalopod beaks were identified with the aid of published catalogues (Clarke, 1962, 1980, 1986; Torno, 1976; Menni et al., 1984; Roper et al., 1984; Boschi et al., 1992; Gosztonyi and Kuba[1]) and a reference collection of otoliths, cephalopod beaks, and crustaceans belonging to the Marine Mammals Laboratory, Centro Nacional Patagónico, CONICET.

The number of individuals of a particular fish species (NF) found in a stomach was calculated as

[1] Gosztonyi, A., and L. Kuba. 1996. Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Plan de Manejo Integrado de la Zona Costera Patagonica (PMIZCP), Global Environmental Facility (GEF), Programa de las Naciones Unidas para el Desarrollo (PNUD), Wildlife Conservation Soc. (WCS), and Fundación Patagonia Natural (FPN) Informe Técnico 4, 29 p.

Manuscript accepted 6 August 1997.
Fishery Bulletin 96:366–374 (1998).

$$NF = LO + 0.5NO, \quad \text{if LO>RO},$$

or as

$$NF = RO + 0.5NO, \quad \text{if RO>LO},$$

where *LO*, *RO*, and *NO* = the number of left, right, and not assigned otoliths respectively.

Minimal number of cephalopods was obtained with maximum count of upper and lower beaks for each species.

All complete and nondigested elements (otoliths and beaks) were measured with digital calipers. Some otoliths or beaks were digested, or broken, and could not be measured. Any otolith was considered too digested to be measured if it presented rounded borders and rostrum, and an ill-defined sulcus. Around 42% of the prey items were represented by broken or digested elements. Size values for these pieces were randomly assigned from sizes of items taken from the stomach and measured. When only broken or digested elements were found in the stomach, the average individual weight of the prey species in the whole sample was used to estimate the individual weight of the items.

The length of prey items was estimated by using regressions between total length (TL) and otolith length (OL) for fishes, and between dorsal mantle length (DML) and lower rostral length (LRL), or lower hood length (LHL), for squids. Wet weight (W) was estimated from regression-estimated length of prey by using regressions between W and TL for fishes, and between W and DML for squids. Regressions for most prey species were developed during this study on the basis of materials collected from commercial hauls. All regressions were calculated as simple linear regressions. Those variables that did not have linear relationships were made linear with natural logarithms (Table 1). The TL and W of *Notothenia* sp. was estimated with *Notothenia angustifrons* regressions (Table 1). The W of *Octopus tehuelchus* was estimated with *Octopus vulgaris* regression between W and LHL (Table 1). The W of each *Semirossia tenera* was assumed to be 3 g, as was the average individual weight recorded for this species in a sample taken onboard a commercial trawler by one of the authors (N.A.G.). In one stomach (that of LO22 dolphin), only fish eye lenses and a few beaks were found. In this case, eye lenses were similar in size to those of anchovy; therefore the an-

Table 1

Equation, sample size (n), and determination coefficient (r^2) of the regressions used to estimate size and weight of prey of dusky dolphins in Patagonia. The variables used in the regressions were otolith length (OL), lower hood length (LHL), lower rostral length (LRL), total length (TL), dorsal mantle length (DML) and wet weight (W). OL, LHL, and LRL are in mm, TL and DML are in cm, and W is in g.

Scientific name	Common name	Equation	n	r^2	Source
Engraulis anchoita	Argentine anchovy	$TL = 2.368 + 3.56\ LO$	79	0.70	This study
		$W = 2.5\ 10^{-3}\ TL^{3.353}$	81	0.93	
Merluccius hubbsi	Argentine hake	$TL = 1.823\ LO^{1.072}$ if $OL<15$	447	0.93	
		$W = 4.76\ 10^{-3}\ TL^{3.061}$ if $OL<15$	469	0.92	This study
		$TL = 1.984\ LO^{1.05}$ if $OL>15$	693	0.91	
		$W = 9.72\ 10^{-3}\ TL^{2.886}$ if $OL>15$	742	0.96	
Stromateus brasiliensis	"pampanito"	$TL = 3.042\ LO^{1.159}$	51	0.98	This study
		$W = 6.418\ 10^{-4}\ TL^{3.917}$	63	0.98	
Notothenia angustifrons	Southern cod	$TL = 4.142\ LO^{0.768}$	22	0.91	Hecht, 1987
		$W = 3.73\ 10^{-6}\ (10\ TL)^{3.16}$	24	0.98	
Illex argentinus	Argentine shortfin squid	$DML = -3.178 + 5.617\ LHL$	27	0.93	This study
		$DML = 8.257\ 10^{-2} + 6.009\ LRL$	63	0.87	
		$W = 9.82\ 10^{-3}\ LDM^{3.238}$	66	0.98	
Loligo gahi	Patagonian squid	$DML = -0.712 + 4.622\ LHL$	98	0.76	This study
		$W = 2.6\ 10^{-2}\ LDM^{2.753}$	102	0.93	
Octopus vulgaris	octopus	$W = e^{1.82 + 3.03\ \mathrm{Ln}(LHL)}$	108	[1]	Clarke, 1986

[1] The determination coefficient of this regression was not available in the original source.

chovy average individual weight was used to estimate the W of these unidentified fishes. This last estimation was made to evaluate the relative contribution by weight of these unidentified fishes.

The "percent frequency of occurrence" (%FO), the "percent total number" (%N), and the "percent total wet weight" (%W) were calculated (Hyslop, 1980; Castley et al., 1991; McKinnon, 1994). The relative importance of each prey species was evaluated with the index of relative importance (IRI) (Pinkas et al., 1971), where the volumetric percentage was replaced by the %W ($IRI=(\%N+\%W)\%FO$) (Castley et al., 1991).

Results

Dolphins used in this study (Table 2) were caught mostly at night in midwater hauls for the shrimp *Pleoticus muelleri*, with the exception of LO10 and LO23 dolphins that were caught in diurnal bottom hauls for shrimp, LO22 dolphin that was captured in a diurnal bottom haul for hake, and LO26 dolphin that was caught by an unknown fishing vessel. The locations of the catches were principally in the Golfo San Jorge (approximately between 45 and 46°30'S), except LO22 dolphin that was captured in the vicinity of Isla Escondida (43°S). There is no information

Table 2

Biological information (sex, size, age, and reproductive status), number of prey species eaten, and most important prey species by weight in the stomach of each dusky dolphin considered in this study. The biological information of females (F) were taken from Dans et al. (1997) and those of males (M) were provided by S.L. Dans.[1] The date of death is approximate and indicates which dolphins were caught in the same fishing trip.

Field number	Date of death	Sex	Length (cm)	Age (years)	Reproductive status	No. of prey eaten	Important prey species in the stomach
LO01	19 Nov 89	F	158	5	immature	3	Argentine anchovy and Argentine shortfin squid
LO02	19 Nov 89	F	157	4	immature	4	Argentine shortfin squid and Argentine anchovy
LO04	27 Apr 90	F	159	6	immature	3	Argentine shortfin squid and Argentine anchovy
LO05	01 Jun 90	F	166.5	6	mature (lactating)	1	Argentine anchovy
LO06	01 Jun 90	F	174	8	mature (resting)	4	Argentine anchovy
LO07	Jul 90	M	169	6	immature	5	Argentine anchovy
LO08	Apr 92	F	161	7	mature (pregnant)	2	Argentine anchovy
LO09	Apr 92	F	174	11	mature (pregnant)	4	Argentine anchovy
LO10	08 Sep 92	F	172	3+	immature	4	Argentine shortfin squid and Argentine hake
LO11	Sep 92	F	172	7+	mature (resting)	4	Argentine anchovy
LO12	Sep 92	F	162	7+	mature (pregnant)	6	Argentine hake
LO13	Sep 92	F	170	8+	mature (resting)	5	Argentine anchovy and hake
LO14	Sep 92	F	167	7+	immature	3	Argentine hake
LO15	11 Mar 93	F	166	5	immature	2	Argentine anchovy
LO16	11 Mar 93	F	174	6	mature (pregnant)	3	Argentine anchovy
LO17	16 Mar 93	F	164	4	immature	2	Argentine anchovy
LO18	06 Apr 94	F	171	5	immature	4	Argentine anchovy
LO19	11 May 93	M	164	8	mature	3	Argentine anchovy
LO20	Sep 93	M	161	9	mature	2	Argentine hake
LO21	02 Sep 93	F	158	3	immature	4	Argentine hake
LO22	30 Oct 93	F	164	3	immature	2	Unidentified fishes
LO23	15 Oct 93	M	169	9	mature	3	Argentine shortfin squid
LO24	Mar 94	M	173	10	mature	4	Argentine anchovy
LO25	Mar 94	M	162	8+	unknown	3	Argentine anchovy
LO26	94	F	161	8	mature	5	Argentine anchovy and hake

[1] Dans, S. L. Laboratorio de Mamíferos Marinos, CENPAT (CONICET), Boulevard 3600, (9120) Puerto Madryn, Chubut, Argentina

about the location of collection of two dolphins (LO07 and LO26). The entire sample was biased toward females and it was composed of immature and mature dolphins (Table 2) (Dans et al., 1997).

Some dolphins in the sample may have been caught in the same haul because fishermen reported that occasionally more than one dolphin are caught. However, when fishermen capture several dolphins in a fishing trip (between 30 and 60 days), they may discard some of them. In these cases it is uncertain whether those dolphins caught during the same fishing trip (same date of death, see Table 2) were caught together in the same haul.

With the exception of one stomach (LO22) which contained fish eye lenses and a few beaks, all others were half full or full. On average (± standard deviation), 3.40 ±1.19 prey species per stomach were found, but only one or two of them were important by weight in the stomach (Table 2). The mean number of prey items per stomach was 148.08 ±137.91, and the mean regression-estimated ingested biomass was 2,675.63 ±1,848.44 g per stomach.

A total of 3,702 prey items belonging to eight species were found in the 25 stomach contents analyzed, including four fish and four cephalopod species. The fish species were Argentine anchovy, *Engraulis anchoita;* Argentine hake, *Merluccius hubbsi;* "pampanito," *Stromateus brasiliensis*, and the southern cod *Notothenia* sp. The cephalopods were Argentine shortfin squid, *Illex argentinus;* Patagonian squid, *Loligo gahi*, the sepiolid *Semirossia tenera;* and common octopus, *Octopus tehuelchus*.

Argentine anchovy was the most important prey species, representing 39% of prey by number, 46% by weight (Table 3). However, the most frequent prey was the Patagonian squid which was present in 84% of stomachs (Table 3). According to the IRI, the second species in importance was the Argentine shortfin squid, followed by the Patagonian squid and the Argentine hake, whereas by weight the second species was hake, followed by Argentine shortfin and Patagonian squid (Table 3). The "pampanito," octopus, and southern cod were of little importance in dusky dolphin diet (Table 3).

The Argentine anchovy had a unimodal length-frequency distribution with a mode at 16 cm (Fig. 1). Individual anchovies eaten by dusky dolphins were mostly of mature sizes (Hansen, 1994).

Both Argentine shortfin and Patagonian squids were consumed at small sizes. Patagonian squids had a modal DML of 3 cm (Fig. 2), and most of them were smaller than 8 cm, a size that corresponded to that of immature squid (Hatfield et al., 1990). The DML frequency distribution of shortfin squid showed two important peaks at 1–2 cm, and 7–8 cm of DML (Fig. 3) which corresponded to juvenile sizes (Brunetti and Ivanovic, 1992).

Argentine hake showed the widest size range (Fig. 4). Its TL frequency distribution showed three peaks at 8 cm, 22–24 cm, and 36 cm in order of importance (Fig. 4). These sizes corresponded to age-0 group, age 1–2 group, and age 2–5 group, respectively (Gaggiotti and Renzi, 1990).

Average individual length of fish eaten by dusky dolphins ranged from 7.54 cm (southern cod) to 19.81 cm (Argentine hake). The DML range for cephalopod preys was estimated to be between 2 cm (observed DML of *S. tenera*) and 6.35 cm (shortfin squid).

Table 3

Relative importance of prey species of dusky dolphins in the Patagonian continental shelf.

	Percent total number (%N)	Percent total wet weight (%W)	Percent frequency of occurrence (%FO)	Index of relative importance (IRI)
Cephalopods				
Illex argentinus	30.71	21.05	68.00	3,520.11
Loligo gahi	20.64	4.58	84.00	2,118.09
Semirossia tenera	3.40	0.57	36.00	142.87
Octopus tehuelchus	0.05	0.00	4.00	0.22
Fishes				
Engraulis anchoita	39.25	46.36	80.00	6,848.60
Merluccius hubbsi	5.19	26.46	48.00	1,518.82
Stromateus brasiliensis	0.14	0.29	12.00	5.05
Notothenia sp.	0.03	0.00	4.00	0.11
Unidentified fishes	0.59	0.70	4.00	5.18
Total	100.00	100.01		

For all prey species, average individual length was smaller than 20 cm.

Average individual wet weights of Argentine shortfin squid, Patagonian squid, Argentine hake, and Argentine anchovy ranged from 4 to 92 g. The Argentine anchovy, Argentine hake, and Argentine shortfin squid had an average individual wet weight (± standard deviation) of 21.34 ±7.49, 92.17 ±121.62, and 12.39 ±33.62 g, respectively.

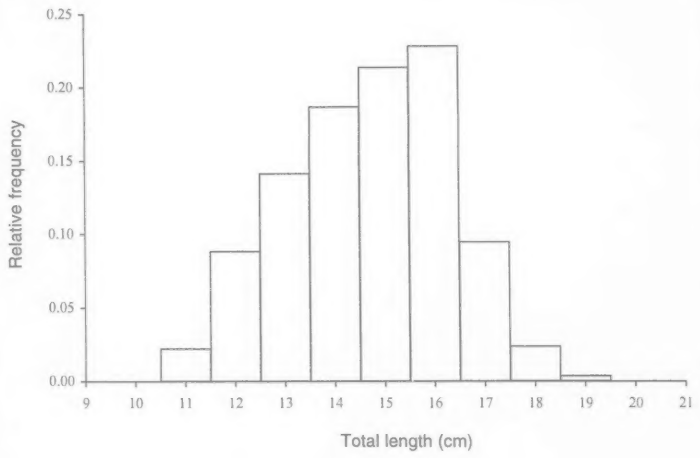

Figure 1

Length-frequency distribution of Argentine anchovy, *Engraulis anchoita*, eaten by dusky dolphins in Patagonia.

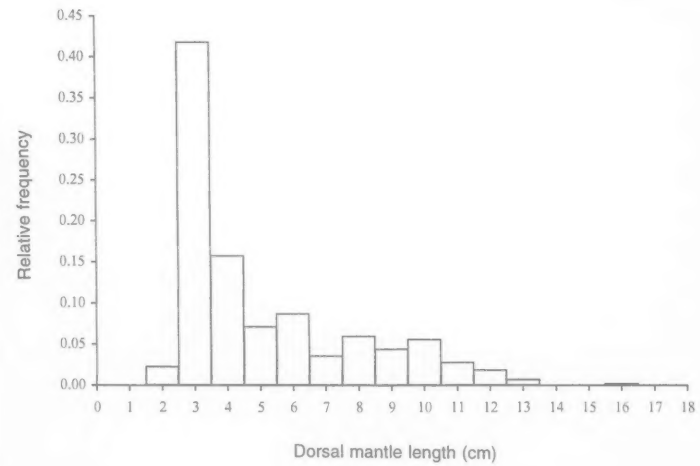

Figure 2

Length-frequency distribution of Patagonian squid, *Loligo gahi*, eaten by dusky dolphins in Patagonia.

Discussion

Patagonian dusky dolphins fed mostly on pelagic species or pelagic stages of demersal species. Argentine anchovy is typically a pelagic species (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990), and Argentine shortfin squid, Patagonian squid, Argentine hake, and "pampanito" are demersal-pelagic species (FAO, 1983; Angelescu and Prenski, 1987; Nigmatullin, 1989; Hatfield et al., 1990; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The sepiolid and southern cod are demersal-benthic species, whereas common octopus is benthic (Roper et al., 1984; Angelescu and Prenski, 1987).

Anchovies are the main food item for dusky dolphins in Argentine and Peruvian waters. *Engraulis ringens* was found to be the principal prey species for dusky dolphins in waters off Peru (McKinnon, 1994), and this study shows that *E. anchoita* is the most important prey species in Argentine waters. Furthermore, squids were the second prey by numbers (*I. argentinus* and *L. gahi* in Argentine waters, and *L. gahi* and *Dosidicas gigas* in Peruvian waters) and hakes were rated second by weight (*M. hubbsi* and *Merluccius gayi* in Argentine and Peruvian waters respectively) (McKinnon, 1994). Moreover, the number of commonly eaten and important prey species (by weight) was quite similar between Argentine and Peruvian dusky dolphins (4 and 6 prey species respectively), considering the difference in the sample size in this work (n=25) and that in McKinnon's (1994) study (n=136). Both populations of the dusky

dolphin feed on ecologically similar species, mostly schooling fishes. However, whereas anchoveta represented 80% in weight of the diet of Peruvian dolphins, Argentine anchovy represented between 40% and 50% in weight of the diet of Argentine dolphins.

Sample size in this study is relatively small and possibly biased by age and sex (Dans et al., 1997; in press). However, our sample included mature and immature dolphins of both sexes, and all the stomach contents were very similar in composition (Table 2). Moreover, dusky dolphins had never been reported to be feeding around fishing vessels on discards and disturbed fish, even when the dolphins in this sample were caught by shrimp trawlers. Furthermore, the diet composition of Peruvian dusky dolphins did not show any difference between sexes or reproductive status (McKinnon, 1994). At Península Valdés, dusky dolphin feeding groups consisted of individuals of both sexes and of almost all age classes (calves and small young could be excluded from the feeding group) (Würsig and Würsig, 1980). Therefore, considering the general similarities in diet composition between Argentine and Peruvian populations, the absence of differences in the diet between sexes and reproductive status in the Peruvian population, the lack of evidence to suggest that dolphins feed on discards and disturbed fishes, and the gregarious feeding behavior of patagonian dusky dolphins described by Würsig and Würsig (1980), we conclude that the sample analyzed in this study is a reasonable indicator of diet composition of dusky dolphins in Argentine waters.

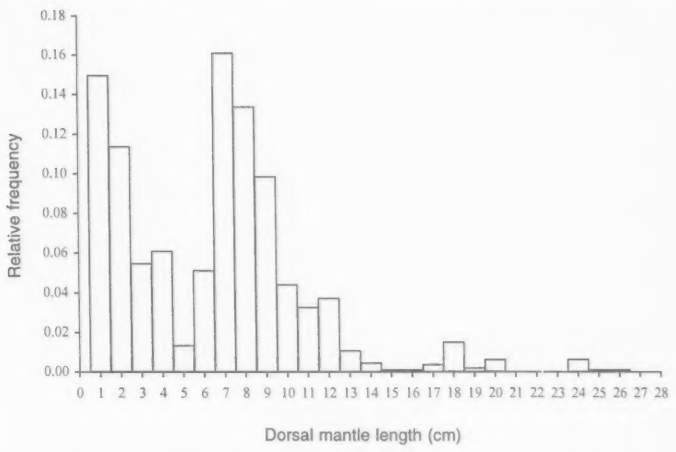

Figure 3

Length-frequency distribution of Argentine shortfin squid, *Illex argentinus*, eaten by dusky dolphins in Patagonia.

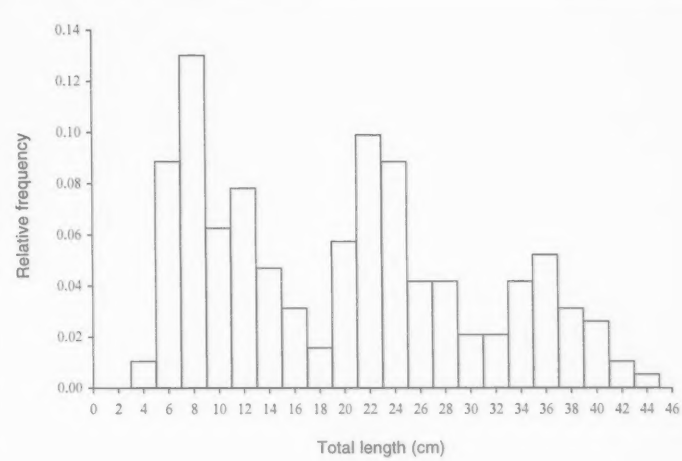

Figure 4

Length-frequency distribution of Argentine hake, *Merluccius hubbsi*, eaten by dusky dolphins in Patagonia.

At least two populations of Argentine anchovy have been reported over the Argentine Continental Shelf: the bonaerensis (northern) and the Patagonian (southern) stocks (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen, 1994). Preadults and adults of the bonaerensis stock migrate northwest from coastal spawning areas to offshore feeding grounds; available information indicates that the Patagonian stock, however, does not show a seasonal migration (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen,

1994). Dolphins in this study were caught off central Patagonia throughout the year between 43°S and 46°30'S; thus dusky dolphins appear to feed on Argentine anchovies from the Patagonian stock. The absence of a well-defined seasonal migration pattern in Argentine dusky dolphins (Würsig and Würsig, 1980) could be related to predation on the Patagonian stock of Argentine anchovy. However, long-distance movements of two dusky dolphins have been recorded after several years in Argentine waters (Würsig and Bastida, 1986).

The Argentine shortfin squid is a neritic-oceanic species, distributed from 30°S to 54°S (Rodhouse and Hatfield, 1990). At least three spawning stocks, 1) the bonaerensis to north Patagonian (early winter), 2) the south Patagonian (winter), and 3) the summer spawning stock (Nigmatullin, 1989; Brunetti et al., 1991; Brunetti and Ivanovic, 1992) have been described over the Argentine Continental Shelf. The latter spends its entire life cycle over the continental shelf, the former two have their spawning grounds on the shelf break and in oceanic waters. Their larvae and juveniles grow and mature over the continental shelf (Nigmatullin, 1989; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The shortfin squids captured by dolphins could belong to any of the spawning stocks because their distributions overlap in the area where dolphins were caught. In addition, the size of squids eaten by dolphins corresponds with that for juvenile squids from all spawning stocks. These juvenile squids are pelagic (Brunetti and Ivanovic, 1992; Ivanovic and Brunetti,1994) and can be found mostly between the 50- and 100-m isobaths (Brunetti and Ivanovic, 1992).

The Patagonian squid is a neritic species and its life cycle is associated with the Malvinas Current over the continental shelf and slope (Hatfield et al., 1990). Its spawning grounds are in shallow and coastal waters, and it migrates to deeper waters to grow, reaching maturity at sizes larger than 10 cm of DML (Hatfield et al., 1990). Patagonian squids eaten by dusky dolphins were mostly of small size; thus feeding on this species could occur as juveniles migrate from the coastal area to deeper feeding grounds beyond the shelf break.

The main TL peak for Argentine hake eaten by dolphins corresponds to the age-0 group. This group exhibits pelagic schooling behavior (Angelescu and Prenski, 1987). Moreover, juveniles do not follow the adult hake migration pattern but remain in their nursery grounds (south of the Golfo San Jorge and Isla Escondida area) (Angelescu and Prenski, 1987).

In sum, these results indicate that dusky dolphins of Patagonia feed mostly on species whose stages exhibit pelagic and schooling behavior.

Finally, Argentine hake, Argentive anchovy, and squids are key species in the trophic web of the Patagonian Continental Shelf ecosystem and seem to present some degree of association (Angelescu and Prenski, 1987). Peneid crustaceans, like the shrimp, appear to be associated with these species in the study area even when their abundance is comparatively less (Angelescu and Prenski, 1987). Shrimp were not found in dolphins stomachs, even when they were caught incidentally in shrimp hauls. There are no data about the behavior of the dolphins at the moment of the catch, but the absence of shrimp in the diet suggests that dolphins avoid shrimp as a prey.

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Preliminary estimate of spawning frequency and batch fecundity of striped weakfish, *Cynoscion striatus*, in coastal waters off Buenos Aires province*

Gustavo J. Macchi

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)
Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)
CC. 175, Mar del Plata (7600), Argentina

E-mail address: gmacchi@inidep.edu.ar

The striped weakfish, *Cynoscion striatus*, is a demersal species inhabiting coastal waters of the Southwest Atlantic. It ranges from Brazil (22°35'S) to the south of Buenos Aires province (Argentina) (42°S) (Cordo, 1986). The commercial catch takes place mainly off Buenos Aires province, between 35° and 40°S, to 50 m depths. The annual catch of this species is about 20,000 metric tons,[1] corresponding to 20% of the total commercial catch of coastal species in Argentina.

Despite a variety of studies describing *C. striatus* life history, such as feeding (Ciechomski and Ehrlich, 1977; Cordo, 1986), growth (Ciechomski and Cassia, 1978), embryonic and larval development (Ciechomski and Cassia, 1982), length distributions, and sex ratios (Cousseau et al., 1986), studies on reproductive biology are rare and largely incomplete. Only one previous report has included histological analysis of the ovaries and fecundity estimates (Cassia, 1986), providing evidence that striped weakfish is a multiple spawner.

In the present study, ovaries of *C. striatus* from the coastal area of the Buenos Aires province (Argentina, Southwest Atlantic) were examined histologically, and particular attention was paid to evidence for multiple spawning and to estimates of spawning frequency and batch fecundity.

Material and methods

Cynoscion striatus was collt\ted in the zone known as "El Rincón" (Buenos Aires province, Argentina, 38°50'–40°30'S) during two research trawl cruises carried out in early November 1994 (n=179) and September 1995 (n=224) (Fig. 1). Mature females caught near "Punta del Este" (Uruguayan coast, 35°10'S–55°W) in November 1994 were also used to estimate fecundity (n=26).

Individuals were measured to the nearest centimeter (total length, TL) and weighed (total weight, TW). Length range of sampled females was 31–58 cm TL, which corresponds to 3–15 yr old individuals (Cioffi, 1992). The decision to sample only females of *C. striatus* greater than about 30 cm was based on the fact that this length is the size at maturity (Macchi and Acha[2]). Immature ovaries therefore were underrepresented in the samples.

The ovaries of individuals sampled were removed immediately after capture and fixed in 10% neutral-buffered formalin or in Davidson's fluid for two weeks. Later, fixed gonads were weighed (GW), and a portion of tissue (about 2.0 g) was removed from the center of each ovary, dehydrated in methanol, cleared in benzol, and embedded in paraffin. Tissues were sectioned at approximately 5 µm thickness, stained with Harris's hematoxylin followed by eosin counterstain. Histological classification of ovaries was based on the occurrence and relative abundance of five stages of oocyte development (Table 1) as well as on the occurrence and intensity of atresia. The terminology used in the description of oocyte stages was adapted from Forberg (1982), and the classification of atresia followed that given by Hunter and Macewicz (1985). Ovaries were classified into eight stages: 1) immature, 2) developing early, 3) developing late, 4) fully developed, 5) gravid, 6) partially spent, 7) spent, and 8) resting. This classification is a modification of that given by Mayer et al. (1988). Oocyte measurements were taken of the ovaries in different maturity stages (3 ovaries for each stage). Oocytes with visible nuclei showing were measured along the longest axes with an ocular micrometer. About 10 fields of view per histological section were chosen at random (Fig. 2).

To estimate the spawning fraction, only the samples collected during November 1994 were used. The percentage of spawning fe-

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males was determined by estimating the incidence of fish with postovulatory follicles (POF) (Hunter and Goldberg, 1980). These structures were classified as day-0, day-1, or day-2 postovulatory follicles, following the description by Goldberg et al. (1984) for *Sardinops sagax* and by Melo (1994) for *Engraulis capensis*.

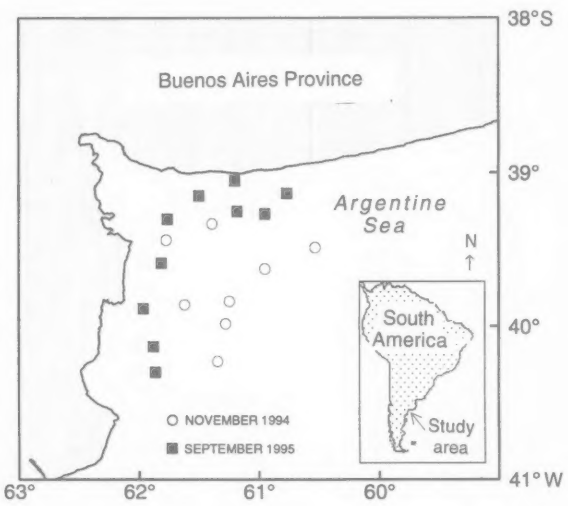

Figure 1

Location where samples of female striped weakfish were collected off "El Rincón" area.

The proportion of spawning females was estimated from the different stages of POF, but the spawning frequency was determinated by taking the average of the percentages of day-0 and day-1 spawning females (Fitzhugh et al., 1993).

Batch fecundity (BF) (number of oocytes released per spawning) was estimated gravimetrically with the hydrated oocyte method (Hunter et al., 1985) on fixed ovarian samples. Hydrated ovaries that contained new postovulatory follicles were not used for this estimation. Batch fecundity was determined for 41 females (17 from "El Rincón" and 24 from the Uruguayan coast). Three 0.1-g tissue subsamples were collected from the anterior, middle, and posterior sections of one ovary of each pair. These subsamples were weighed to the nearest 0.00001 g. All hydrated oocytes in each subsample were counted under stereoscopic microscope (magnification of 6×). Batch fecundity for each female was the product of the mean number of hydrated oocytes per unit weight and the total weight of the ovaries. Relative fecundity (RF) (hydrated oocytes per gram of body weight) was calculated as the batch fecundity divided by female weight (without ovary). To compare the "El Rincón" data with those from the Uruguayan coast, the length ranges coincident with the two zones were truncated between 40 and 50 cm TL ("El Rincón," n=15; Uruguayan coast, n=17). The fecundity values and the coefficients of the batch fecundity to

Table 1

Morphological changes observed in the different oocyte growth phases. Adapted from Forberg (1982).

Oocyte growth stages	Description
First growth phase Cromatin nucleolus stage Early nucleolus stage Late nucleolus stage	Previtellogenic oocytes with diameters smaller than 100 µm. Cytoplasm is basophilic and the nucleus shows a number of nucleoli situated peripherally. Follicular cells are flattened and become visible on the outer surface of oocyte.
Second growth phase Yolk vesicle stage	Diameter ranged between 100–250 µm. Cytoplasm is basophilic and shows small uncolored vacuoles (yolk vesicles). Granulosa and follicular thecae are distinguished and the zona radiata becomes visible around the periphery of oocyte.
Primary yolk stage	Diameter ranged between 250 and 350 µm. Numerous eosinophilic yolk globules appear between the yolk vesicles. These yolk globules are composed mainly of proteins. The zona radiata and the follicle epithelium are more prominent.
Secondary yolk stage	Diameter between 400 and 600 µm. The yolk globules have multiplied and increased in size, occupying all the cytoplasm. The nucleus exhibits an irregular shape, and the zona radiata increases in thickness.
Tertiary yolk stage or final oocyte maturation	Oocyte diameter ranged between 600 and 700 µm. In the first instance, the nucleus is displaced to the animal pole (migratory nucleus stage). The nuclear membrane disintegrates and the yolk globules tend to coalesce. In the section, these oocytes appear with a cytoplasm weakly eosinophilic and an irregular shape.

total length relationships obtained for both areas were compared with a test of equality of means and a test of equality of coefficients (Draper and Smith, 1981). The relations of batch fecundity to total length and total weight (without ovary) were assessed with regression analysis (Draper and Smith, 1981). Significance of these relations were evaluated by testing if the slope of the regression was significantly different from zero.

Results

Oocyte diameter distributions of different maturity stages (immature to gravid) of *C. striatus* show that this species is a multiple spawner (Fig. 2). The gravid ovaries show four main groups of oocytes. The first group is composed mainly of primary growth oocytes (smaller than 100 µm). The second group is composed of partially yolked oocytes in several stages ranging approximately from 100 to 300 µm. The third group is formed by advanced yolked oocytes ranging between 400 to 600 µm. The fourth group corresponds to the hydrated oocytes between 600 to 700 µm.

During September, 95% of the females were found in the developing stages (early and late), with a small percentage (3%) in the fully developed phase (Fig. 3). The samples obtained during early November were composed mainly of females in the partially spent stage with postovulatory follicles; about 11% of the samples were gravid females. These results indicate that the beginning of spawning of *C. striatus* in "El Rincón" is in October.

Of the mature females taken in November, 12% had hydrated oocytes, 11% had new postovulatory follicles (phase 0), 13% had day-1 postovulatory follicles, and 11% had old postovulatory follicles (phase 2) (Table 2). Therefore, each female was calculated to spawn every 7–9 days. The average of the percentages of day-0 and day-1 spawning females was

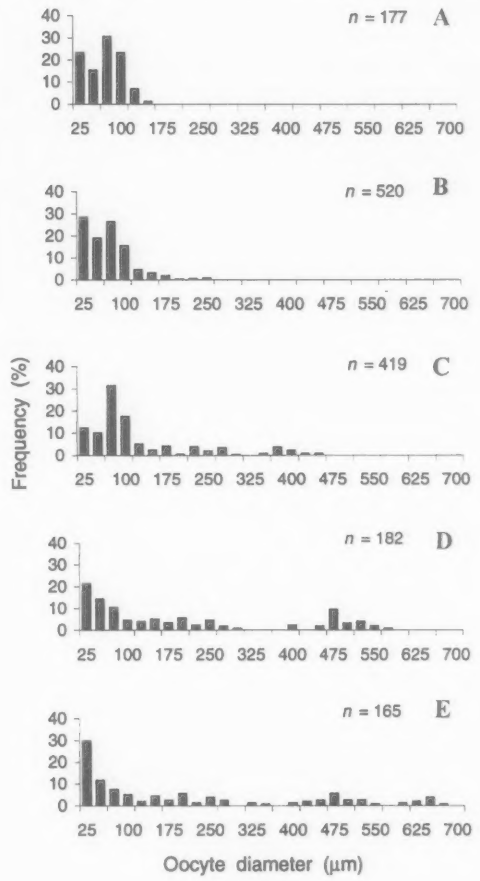

Figure 2

Oocyte diameter distributions for different maturity stages: A = immature; B = developing early; C = developing late; D = fully developed; and E = gravid.

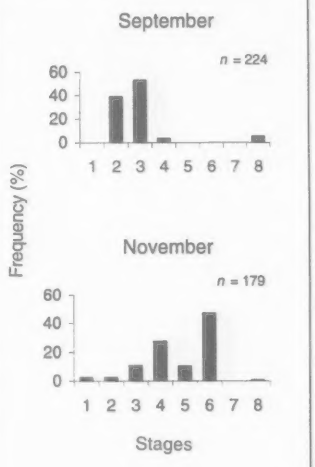

Figure 3

Maturity-stage frequency of striped weakfish during September 1995 and November 1994. Stages: 1 = immature; 2 = developing early; 3 = developing late; 4 = fully developed; 5 = gravid; 6 = partially spent; 7 = spent; and 8 = resting.

Table 2

Number of reproductively active females of *C. striatus* sampled in "El Rincón" area based on histological staging for determination of spawning frequency. POF = postovulatory follicles; CI = confidence interval.

Day of month (November)	Hydrated oocytes	POF day-0	POF day-1	POF day-2	Total mature
2	1	2	2	4	23
3	3	2	2	5	28
3	1	3	4	1	13
3	5	1	0	1	13
4	0	1	8	5	27
5	4	7	1	2	22
5	1	0	0	2	17
6	2	3	4	1	17
8	1	0	2	0	12
Total	18	19	23	21	172
% (average)	11.71	11.09	13.44	10.65	
95% CI	12 ±7	11 ±7	13 ±8	11 ±4	

12% (±6), which yielded an estimation that spawning occurred every 8 days.

The range in batch fecundity for females caught in "El Rincón" was 50,000 to 450,000 hydrated oocytes for fish between 40 and 53 cm TL. The samples collected from the Uruguayan coast ranged from 38,000 to 360,000 hydrated oocytes for females of 34 to 52 cm. A test of equality of means for the batch fecundity values of both zones showed no significant difference ($P>0.56$). A test of equality of coefficients indicated that no significant difference existed between the equations for BF vs. TL for the two areas ($P>0.05$). The general equations for the total length and total weight were determined by combining all data (Fig. 4, A and B). No statistical differences were observed between the mean values of relative fecundity obtained for both zones ($P>0.25$). This parameter ranged between 50 and 420 hydrated oocytes per gram of female (ovary free); an increase in the number of oocytes with size was observed (Fig. 4, C and D).

Discussion

The results obtained indicate that striped weakfish is a multiple spawner with indeterminate annual fecundity. Hence, the potential annual fecundity is not fixed prior to the onset of spawning, and unyolked oocytes continue to mature and to be spawned during the reproductive season (Hunter et al., 1992). This assumption is based on two lines of evidence: 1) the presence of maturing ovaries with postovulatory follicles (partially spent stage), which indicates that after spawning one batch of eggs, a new batch develops and is released; and 2) oocyte size frequency, which shows a continuous distribution of growing vitellogenic oocytes.

Reproductive activity of striped weakfish in the coastal waters of Buenos Aires province ranges from October to March, with a main peak in November (Cassia, 1986). The histological examination of ovaries obtained during September did not show evidence of spawning, but those taken in early November indicated considerable reproductive activity, with a high proportion of postovulatory follicles and the appearance of hydrated oocytes. This corroborates the hypothesis that the spawning of *C. striatus* in "El Rincón" area generally begins in October. Unfortunately, it was not possible to sample this species during the rest of the spawning season, which lasts about 6 mo. according to Cassia (1986). The long reproductive season of this species has also been observed in other sciaenids inhabiting temperate waters, such as *Seriphus politus* (7 mo.) (De Martini and Fountain, 1981), *Cynoscion nebulosus* (7 mo.) (Brown-Peterson et al., 1988), *Micropogonias undulatus* (7 mo.) (White and Chittenden, 1977; Barbieri et al., 1994), *Genyonemus lineatus* (7 mo.) (Love et al., 1984), *Cynoscion nothus* (6 mo.) (De Vries and Chittenden, 1982) and *Cynoscion regalis* (5 mo.) (Merriner, 1976). In Argentinian coastal waters, the main sciaenid associated with *C. striatus* is the white croaker (*Micropogonias furnieri*), which has reproductive activity from November to March (Macchi and Christiansen, 1996).

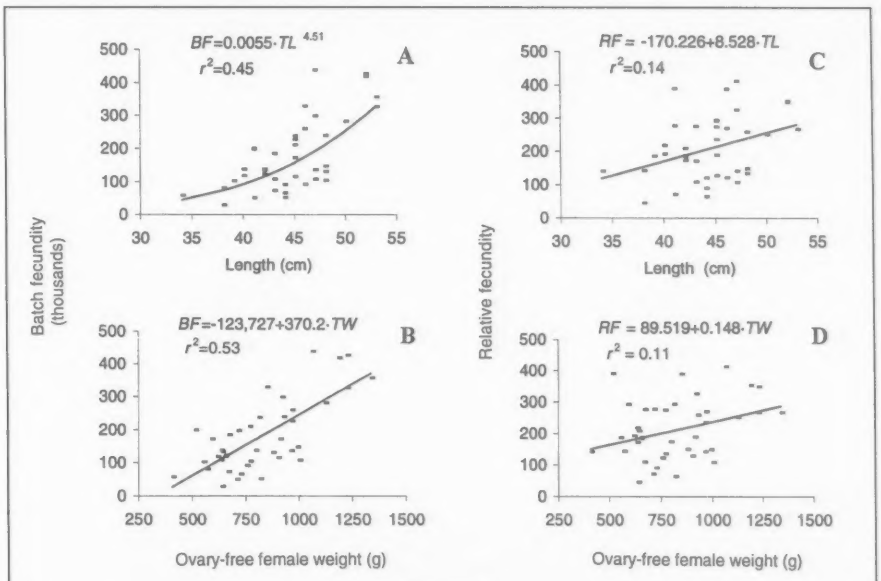

Figure 4

Batch fecundity as a function of total length (**A**) and total weight (without ovary) (**B**). Relative fecundity as a function of total length (**C**) and total weight (without ovary) (**D**).

Because vitellogenic oocytes are recruited continually during the reproductive season, it is necessary to determine the batch fecundity and the number of spawnings in the season in order to estimate total egg production (Hunter et al., 1985). Spawning frequency estimated from the percentage of hydrated ovaries (12%) was similar to those calculated with postovulatory follicles (11–13%). The average between day-0 and day-1 POF's (12 ±6%) indicates that spawning occurred once every 8 days during the main peak of the reproductive season (November). Daily spawning fraction of *C. striatus* was similar to that reported for three other scienids: *Seriphus politus* (De Martini and Fountain, 1981), *Genyonemus lineatus* (Love et al., 1984) and *Cynoscion nebulosus* (Brown-Peterson et al., 1988), but was lower than estimates for *Pogonias cromis* (31%) (Fitzhugh et al., 1993). Annual spawning frequency estimated for *Sciaenops ocellatus* (Wilson and Nieland, 1994) and *Cynoscion regalis* (Lowere-Barbieri et al., 1996) varied widely, 3 to 80 days and 2 to 13 days, respectively. Daily spawning percentage of white croaker (*Micropogonias furnieri*) in the Southwest Atlantic was 8.83% (Macchi et al., in press), indicating that the average interval between spawnings for this sciaenid is about 12 days .

Cassia (1986) estimated total fecundity for *C. striatus* by counting the number of growing oocytes, which is inappropriate for a multiple spawning species (Hunter and Goldberg, 1980). This author estimated a total fecundity of 600,000 oocytes for one 40-cm-TL female, when the batch fecundity for that length is about 100,000 hydrated oocytes. In the present study, analysis of variance applied to the fecundity data from "El Rincón" and the Uruguayan coast indicated no statistical differences between these areas. Batch fecundity was a power function of length and a linear function of ovary-free body weight and ranged between 50,000 (34 cm TL) and 450,000 (53 cm TL) hydrated oocytes. Batch fecundity values estimated for striped weakfish were higher than those obtained for smaller sciaenids, such as *Genyonemus lineatus* (800–37,200 oocytes) (Love et al., 1984) and *Seriphus politus* (5,000–90,000 oocytes) (De Martini and Fountain, 1981). Sciaenids with length ranges similar to *C. striatus*, such as *Cynoscion regalis* (Lowere-Barbieri et al., 1996) and *Cynoscion nebulosus* (Brown-Peterson et al., 1988), show slightly higher batch fecundity values. The relations between batch fecundity vs. length and batch fecundity vs. weight for these species had relatively low coefficients of determination, similar to those for striped weakfish. The mean relative fecundity for *C. striatus* (210 ±35 oocytes/g ovary-free body weight) was less than that obtained for *Cynoscion nebulosus* (451 ±43 oocytes) (Brown-Peterson et al., 1988) and

Cynoscion regalis (200–750 oocytes) (Lowere-Barbieri et al., 1996).

Accurate annual fecundity estimations are difficult to determine for multiple spawning fishes with an extended reproductive season (Brown-Peterson et al., 1988). During November–March, a female *C. striatus* would spawn 22 times with a spawning frequency of 8 days. Consequently, annual fecundity estimates for a 40.0-cm-TL female would be about 2.0 million eggs. However, annual egg production depends on spawning frequency, and it is possible that this parameter varies during the reproductive season and between years (Lowerre-Barbieri et al., 1996). The annual fecundity estimate for *C. striatus* was similar to that obtained for white croaker of the Rio de la Plata estuary (*Micropogonias furnieri*) (1.8 million eggs for a 40.0 cm TL female) (Macchi et al., in press). Both species are among the most heavily exploited coastal resources in Argentina and Uruguay.

Acknowledgments

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Direct validation of ages determined for adult black drum, *Pogonias cromis*, in east-central Florida, with notes on black drum migration

Michael D. Murphy
Florida Marine Research Institute, Department of Environmental Protection
100 Eighth Avenue
St. Petersburg, Florida 33701-5095
E-mail address: murphy_m@harpo.dep.state.fl.us

Douglas H. Adams
Derek M. Tremain
Florida Marine Research Institute, Department of Environmental Protection
1220 Prospect Avenue, Suite 285
Melbourne, Florida 32901

Brent L. Winner
Florida Marine Research Institute, Department of Environmental Protection
100 Eighth Avenue
St. Petersburg, Florida 33701-5095

Findings from indirect age validation studies, in which marginal increments in black drum, *Pogonias cromis*, otolith sections were examined, indicate that the number of opaque bands observed in otoliths is a measure of the true age in years of black drum (Murphy and Taylor, 1989; Beckman et al., 1990; Beckman et al.[1]). However, validation studies of scale-determined ages have indicated that more than one mark is deposited on black drum scales each year after they reach about age four (Richards, 1973; Cornelius, 1984). In addition, evidence from an analysis of the marginal increments for a related sciaenid, the croaker *Micropogonias opercularis*, has indicated that more than one opaque band was deposited on its otoliths each year (Haimovici, 1977).

Unlike indirect validation studies which provide estimates of the periodicity of annulus formation for a sample of fish, mark-recapture studies provide proof of the accuracy of an age determination technique for an individual fish during the period of time between marking and recapture (Beamish and McFarlane, 1983). This direct technique has been used to validate ages for a variety of species, including red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991; Ross et al., 1995); snapper, *Pagrus auratus* (Francis et al., 1992); sablefish, *Anoplopoma fimbria* (McFarlane and Beamish, 1995); and the tropical parrotfish *Scarus schlegeli* (Lou, 1992). Because mark-recapture studies provide information on the validity of age marks formed since the mark was applied, they cannot be extrapolated to imply the validity of younger ages (Francis, 1995).

In assessing the status of black drum stocks, accurate age determination is especially critical. These fish are suspected to live to about 60 years old, and the large fisheries that they have supported apparently exploited infrequent, large year classes (Jones et al., in press; Beckman et al.[1]). The purpose of this study was to validate directly the ages of adult black drum by using mark-recapture methods. The sample of recaptured fish also provided insight into the population dynamics of black drum in east-central Florida.

Materials and methods

We used a 549-m nylon trammel net (124- and 356-mm mesh, inside and outside stretch, respectively) to capture adult black drum in the southern Mosquito Lagoon and northern Banana River areas of the Indian River Lagoon system along Florida's Atlantic coast (Fig. 1). Black drum were captured for tagging in February, June, and September 1992, and in February, June, and August 1993. Each fish was measured for total length (mm), tagged with a 100-mm Hallprint plastic dart tag, injected intramuscularly with approximately 25 mg of oxytetracycline (OTC) per kilogram of body weight, and released to the capture area. The dart tag was placed in the side of the fish about 25 mm ventral to the anterior insertion of the second dorsal fin. This placement allowed the barb to lodge behind a pterygiophore while leaving the external message (streamer) visible. This external streamer bore an identification number and a message in-

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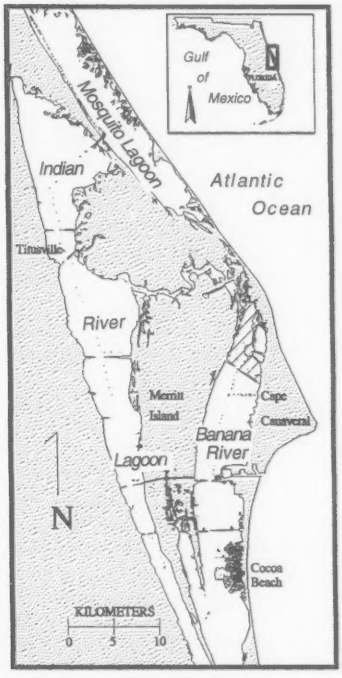

Figure 1

Sampling area for black drum along the Atlantic coast of Florida. Most sampling was done in the area shown by diagonal lines just west of Cape Canaveral. Some sampling was also done in the southern portion of Mosquito Lagoon.

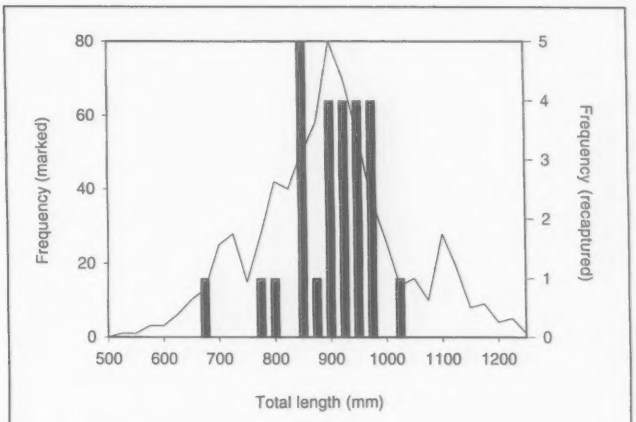

Figure 2

Total length-frequency distribution (mm) for black drum that were tagged and released (line, n=707) and for those that were recaptured (bars, n=26).

structing anglers to contact us. The OTC provided a reference mark defining the otolith margin at the time of initial capture; all recaptures of fish whose otoliths were recovered were made by biologists during sampling trips conducted in August 1993 and January, October, and December 1995.

Recaptured fish were sacrificed and returned to the laboratory, where they were measured for total, fork, and standard lengths; weighed to the nearest tenth of a kilogram; and sexed macroscopically. Sagittal otoliths were excised and stored dry. An Isomet low-speed saw was used to make transverse cuts near the core of the whole otolith. Otolith sections were about 0.5-mm thick and were mounted on glass slides with coverbond mounting media. Opaque bands and OTC marks were examined with a compound dissecting microscope (4× magnification) equipped with an ultraviolet light source. Distances from the otolith core to the proximal edge of the OTC mark and to each opaque band distal to the OTC mark were measured along the axis from the core to the ventral edge of the sulcus acousticus with the aid of an Optimus digital-image processing system.

Results and discussion

A total of 707 adult black drum, from 515 to 1,237 mm TL, were captured, injected, and tagged during this study. Twenty-six of these fish were recaptured, and their otoliths were excised. Lengths of recaptured black drum ranged from 656 to 1,011 mm TL (Fig. 2). Most of the large (>1,050 mm TL) adult black drum found in our sample came from a school of very large fish caught in southern Mosquito Lagoon; according to two tag returns (see below), this school had apparently left the area shortly after tagging and release.

Ages of recaptured black drum ranged from 3 to 13 years (Table 1); 16 were age 8 and older and were likely to have been mature adults at time of recapture (Murphy and Taylor, 1989). Time-at-large for recaptured fish was from just over a month to just less than three years, i.e. 42–1,031 days.

Observations of the number of opaque bands deposited since the fish had been marked supported our hypothesis that one band formed each year from the late winter to early spring. We observed that five fish tagged during February or June 1993 and recaptured 42–176 days later in August 1993 had not deposited an opaque band since being marked (Table 1). One fish at large for 555 days between June 1993 and January 1995 had deposited one band since release. All other fish recaptured had been at large for 805 to 1,031 days, during which two late-winter to early-

Table 1

Tag, recapture, and otolith-measurement data for OTC-marked black drum. Otolith measurements were made from the core to the proximal edge of the OTC band and all subsequent opaque bands to the otolith edge along the ventral margin of the sulcus acousticus.

Tagged		Recaptured				Distance from otolith core (mm)			
Date	Total length (mm)	Date	Total length (mm)	Days free	Age (yr)	OTC mark	Annulus	Annulus	Otolith edge
Jun 93	660	Aug 93	656	42	3	2.33			2.35
Feb 93	836	Aug 93	838	176	5	2.75			2.86
Feb 93	975	Aug 93	945	176	11	3.99			4.08
Feb 93	925	Aug 93	921	176	11	3.85			3.90
Feb 93	940	Aug 93	926	176	11	3.79			3.86
Jun 93	732	Jan 95	790	555	4	2.39	2.65		2.81
Aug 93	832	Oct 95	887	805	13	3.56	3.62	3.74	3.93
Aug 93	899	Oct 95	968	805	9	3.44	3.50	3.68	3.87
Aug 93	922	Oct 95	961	805	13	3.75	3.81	3.95	4.11
Jun 93	711	Oct 95	826	847	5	1.74	1.83	2.04	2.31
Feb 93	975	Oct 95	1,011	991	13	3.61	3.75	3.94	4.13
Aug 93	821	Oct 95	859	805	13	3.73	3.77	3.93	4.09
Feb 93	873	Oct 95	886	981	9	3.00	3.16	3.29	3.51
Aug 93	925	Oct 95	952	805	13	4.03	4.08	4.23	4.40
Feb 93	673	Oct 95	842	981	6	2.50	2.63	2.86	3.10
Jun 93		Oct 95	903	847	5	2.44	2.55	2.81	3.03
Aug 93	832	Oct 95	843	805	13	3.77	3.80	3.96	4.11
Aug 93	941	Oct 95	943	805	13	3.95	4.00	4.17	4.33
Aug 93	852	Oct 95	886	805	13	3.98	4.02	4.15	4.29
Jun 93	620	Oct 95	771	847	5	2.37	2.55	2.83	3.06
Feb 93	880	Dec 95	965	1,031	9	3.30	3.45	3.67	3.92
Feb 93	892	Dec 95	936	1,031	13	3.78	3.90	4.03	4.20
Aug 93	782	Dec 95	899	855	6	2.99	3.08	3.40	3.67
Feb 93	790	Dec 95	911	1,031	7	2.79	2.96	3.18	3.44
Aug 93	789	Dec 95	917	855	8	3.24	3.28	3.53	3.76
Aug 93	690	Oct 95	830	806	5	2.55	2.64	2.91	3.24

spring periods of opaque band formation had occurred. All of the latter had deposited two bands on their otoliths (Fig. 3).

Our direct validation for most ages from 3 years to 13 years indicates that for young adult black drum, at least, age can be determined accurately by counting saggital otolith annuli. Our results extend the findings of an indirect validation study that had used the periodicity of marginal increments as evidence for validation of ages for black drum up to age four in northeast Florida (Murphy and Taylor, 1989). In addition, the seasonal appearance of opaque margins on the otolith sections in older black drum between 20 and 37 years old in the northern Gulf of Mexico (Beckman et al., 1990) is evidence for the validity of this aging technique in older fish. In contrast, the formation of two growth increments or marks per year on scales appears to begin at the time of maturity; formation of the second mark has been attributed to spawning (Richards, 1973). All black drum larger than 700 mm FL (717 mm TL) and more than four years old that were sampled in the northern Gulf of Mexico (Nieland and Wilson, 1993), and all black drum larger than 650 mm TL and more than 5 years old sampled off northeast Florida (Murphy and Taylor, 1989) were mature. Because our samples included adult fish of these sizes and ages, they were likely mature. Therefore black drum in our sample had clearly deposited only one opaque band on the sagittae each year for a number of years after they first matured. It seems likely then that, unless black drum begin to deposit multiple annuli each year after they attain some age older than that found in our samples, their maximum age would be at least equal to the highest reported opaque band count, about 60 for black drum in U.S. Atlantic coastal waters (Murphy and Taylor, 1989; Jones et al., in press).

Our relatively small sample of validated ages for black drum lends support to previous findings of highly variable year-class strength for this species, and for the generally rapid growth of some fishes inhabiting the Indian River and Mosquito Lagoons. Eleven of the 26 black drum we recaptured were members of the 1982 year class, the oldest year class

in our sample. Beckman et al.[1] also noted the persistence of several large year classes (the 1979, 1974, 1970, and 1966 year classes) in the purse-seine fishery catch in the northern Gulf of Mexico, during 1986–89, and Jones et al. (in press) noted that the exceptionally large 1942 and 1934 year classes were still prominent in 1990–92 samples collected from Chesapeake Bay fisheries. Observed sizes at age of black drum in our sample, when released, were 620–732 mm TL for 3 year olds, 782–836 mm for 4 year olds, and 789–880 mm for 6 year olds. These sizes at age were much larger than those predicted for northeast Florida black drum: 477, 555, 625, and 687 mm TL for ages 3–6 (Murphy and Taylor, 1989). Young red drum, *Sciaenops ocellatus,* and spotted seatrout, *Cynoscion nebulosus*, are also larger at age in the Indian River Lagoon than in other areas of Florida (Murphy and Taylor, 1990, 1994).

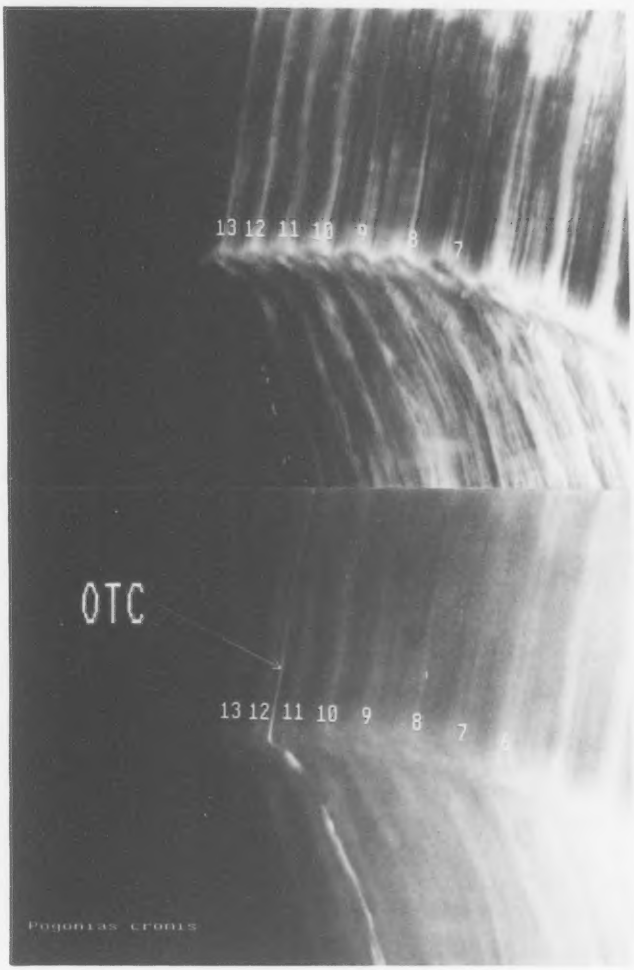

Figure 3

A black drum otolith section shown under reflected light only (top) and under reflected light and ultraviolet light (bottom). Opaque bands are numbered consecutively from the core, and the fluorescing oxytetracycline (OTC) band is indicated. This fish was tagged and injected in August 1993 and recaptured 941 days later in October 1995.

Limited tag-recapture information gathered during this study indicates that some larger black drum make extensive migrations from the Indian River Lagoon system. Seven of the 9 angler-recaptured, tagged black drum (none of whose otoliths were recovered) were caught in the northern Indian River Lagoon within 10 km of their release site. Two fish (1,025 and 1,163 mm TL), however, tagged and released in February 1992 travelled about 1,370 km north to Chesapeake Bay, where they were captured by anglers in late May and early June. Although the reproductive states of these two tagged fish were not recorded at release, many of the males tagged along with them were running ripe. The fact that these fish moved to Chesapeake Bay during the time period when peak spawning progresses up the Atlantic coast may imply that black drum continue spawning as they move northward during the spring. This migration would enable them to broadcast their average annual fecundity of 32–45 million eggs (Fitzhugh et al., 1993; Nieland and Wilson, 1993) over a wide range of suitable egg and larval habitats.

Extensive tagging studies in Florida during the early and mid-1960's showed that, except for some of those released on beaches, black drum hardly moved from a release site (Topp, 1963; Beaumariage, 1964, 1969; Beaumariage and Wittich, 1966); even the greatest movement of fish along the beaches was less than 145 km. The total lengths of fish tagged during these studies were generally less than 500 mm. In Texas, Osburn and Matlock (1984) found substantial intrabay movement of small immature black drum, but little movement between bays. Music and Pafford (1984) also found that most black drum tagged in Georgia did not move far from the area of release. However, in Georgia 13% of all returned fish

had moved more than 100 km, reaching as far south as West Palm Beach, Florida (619 km), and as far north as Murrells Inlet, North Carolina (437 km). Surprisingly, the two black drum that had travelled the farthest from their release sites in Georgia were less than 350 mm TL.

Because black drum are long-lived and capable of extensive movements, knowledge about the magnitude and frequency of their mixing during their potential 60-year life span is critical for understanding how fishing pressure within one geographic area affects fish populations in other areas. In Florida, strict regulations on the harvest of black drum were implemented in 1989 following unvalidated evidence that they were long-lived fish (Murphy and Taylor, 1989). Because many current stock assessment techniques often depend on an accurate estimate of maximum life span so that a natural mortality rate for a population can be determined, validation studies are especially critical in helping to prevent mismanagement of long-live species (Beamish and McFarlane, 1983).

Acknowledgments

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The influence of spear fishing on species composition and size of groupers on patch reefs in the upper Florida Keys

Robert D. Sluka*
Kathleen M. Sullivan

Department of Biology, University of Miami
Coral Gables, Florida 33124

and

Florida and Caribbean Marine Conservation Science Center
The Nature Conservancy
P.O. Box 249118, Coral Gables, Florida 33124
*Present address: Oceanographic Society of Maldives
P.O. Box 2075, Malé, Republic of Maldives

E-mail address (for K. M. Sullivan, contact author): sullivan@benthos.cox.miami.edu

Groupers are an important fishery resource throughout tropical and subtropical regions of the world (Heemstra and Randall, 1993). Dependent and independent fishery surveys of grouper populations in south Florida and the Caribbean have shown drastic declines in populations, most likely due to intense fishing pressure (Sadovy, 1994; Bohnsack et al., 1994). Combined grouper species landings by weight have declined in the Florida Keys by more than half since the mid 1980's (Bohnsack et al., 1994).

Fishermen tend to target the larger fish in a population, with the result that a decrease in the density, average size, and relative abundance of exploited species is inevitable (Bohnsack, 1982; Russ, 1985; Plan Development Team (PDT), 1990; Roberts and Polunin, 1991). Grouper populations are especially sensitive to fishing pressure, exhibiting reductions in density and average size, as well as shifts in species composition between sites that are fished and those that are unfished (Russ, 1985). For example, the mean weight of three species of grouper was found to be significantly greater in unfished than in fished sites in the Red Sea (Roberts and Polunin, 1993). Similarly, the density and biomass of groupers was significantly greater in sites protected from fishing than in sites unprotected in the Philippines (Russ and Alcala, 1989). Craik (1981) found that a commercially important grouper (*Plectropomus leopardus*) on the Great Barrier Reef had a higher mean size at an unfished reef than at a fished reef. Russ (1985) and Craik (1981) observed that larger individuals of a grouper species were abundant only at unfished reefs. Sluka et al. (1997) showed that the biomass, average size, and reproduction (the total number of eggs produced per hectare) of Nassau grouper, *Epinephelus striatus*, was significantly greater inside a marine fishery reserve than outside. Many studies have attributed a change in the relative abundance of grouper species to fishing pressure (Goeden, 1982; Bohnsack, 1982; Russ, 1985; Watson and Ormond, 1994; Sluka, 1995).

In the Florida Keys there has been a history of management measures that have affected fishing pressure on groupers. In 1980, the state of Florida banned fish traps in its waters (<3 nautical miles), and in 1992 the United States government banned fish traps in federal waters of the Florida Keys (>3 nautical miles to the 150 fathom depth contour). During this study, there was a bag limit of five fish and a minimum size limit of 51 cm (20 in.) for six grouper species (red grouper, *Epinephelus morio*, black grouper, *Mycteroperca bonaci*, yellowmouth grouper, *M. interstitialis*, gag, *M. microlepis*, scamp, *M. phenax*, and yellowfin grouper, *M. venenosa*). Harvest of two species (jewfish, *E. itajara*, in 1990 and Nassau grouper, *E. striatus*, in 1991) has been prohibited in the south Atlantic waters of the United States. Reefs within Key Largo National Marine Sanctuary (KLNMS) and John Pennekamp Coral Reef State Park (JPCRSP) have been protected from spear fishing since 1960. Since the time of this study, the entire Florida Keys has come under the management of the Florida Keys National Marine Sanctuary.

One of the results of the previous management scheme is that the upper Florida Keys can be divided into two areas: one area protected from spear fishing and the other unprotected from spear fishing. It is assumed that the intensity of hook-and-line fishing is similar inside and outside of KLNMS and JPCRSP. Thus the goal of this study was to examine the influence of spear fishing on the size and species composition of groupers in the upper Florida Keys and to discuss potential implications for the management of these populations. These population parameters were

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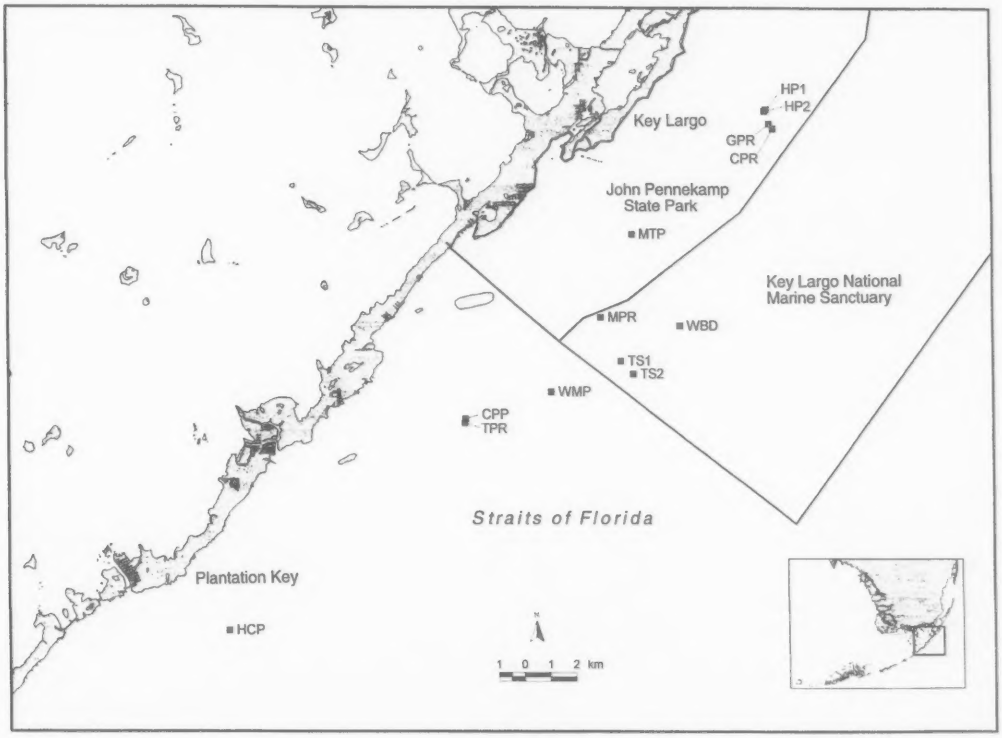

Figure 1

Map showing survey sites located in the upper Florida Keys.

expected to differ between sites under differing fishing intensities owing to the biology of the species, their site-attached nature, and the susceptibility of these species to fishing pressure.

Materials and methods

Sampling on four patch (shallow-water, small) reefs occurred in February 1992, April 1993, September 1993, January 1994, April 1994, and September 1994. Nine additional patch reefs were sampled in September 1994. A total of 13 patch reef sites were sampled (Fig. 1). There were no significant seasonal differences in the size distribution of all grouper species combined at these sites (Sluka and Sullivan, 1996). Thus, data from all seasons were combined for analyses.

Researchers were trained to estimate lengths of fish consistently and accurately using methods outlined in Bell et al. (1985). Observers had approximately five minutes to estimate the length of a series of fish models of varying lengths. The length of each model was recorded in one of five categories: <5 cm, 5–15 cm, 16–25 cm, 26–35 cm, and >35 cm. The frequency distribution of estimated model lengths was compared to the known distribution by using a chi-square test. The bias of each observer was determined as either consistently underestimating or overestimating the size of the fish models. The information on biases was given to each observer. The observer then repeated the length estimation procedure until there was no significant difference between the observed and expected distributions ($P>0.05$). Observers were found to be competent for length estimation after 2–3 trials.

At four of the sites (MPR, TS1, TS2, and HCP), transect lines of 20 m or 25 m in length were used to sample the number, species, and length of groupers. The transect lines were laid in representative portions of each patch reef. The transect line was searched 6 m out from each side for a total width of 12 m (width by visual estimation). Within each transect all groupers were enumerated and their length category and species recorded on underwater paper. Observers using SCUBA searched throughout the width of the transect, examining all crevices, caves, and holes. At the other nine sites, observers sampled the entire patch reef. Patch reef size was not quantified at these sites; thus density could not

be compared between protected sites and those unprotected from spear fishing.

It was hypothesized that spear fishermen were targeting some species more than others owing to their larger size. Targeted species were assumed to be red grouper, black grouper, scamp, and gag. The latter two species were rare, constituting <14% of individuals observed by site. Nassau grouper were assumed to be a nontargeted species because of the ban on harvest. Differences in the relative abundance of targeted grouper were assessed with a t-test on the arcsine-transformed percentage of the total number of grouper observed at a site. Individual sites were the replicates for the analysis.

It was also hypothesized that the average size of targeted species would be significantly different between protected sites and those unprotected from spear fishing. A nested ANOVA was used to test this hypothesis, with the main factor being protection level (spear fished or protected) and sites nested within protection level. The mid points of size categories were used as an estimate of the individual sizes of sampled fish. Thus, for this analysis, individual fish sizes were the replicates. A value of 40 cm was used for individuals in the >35 cm category. This results in a conservative analysis because many of the fish in this category were much larger than 40 cm (R. Sluka, personal observation).

Results

There was no significant influence of spear fishing on the relative abundance of targeted grouper species (t=0.658, P>0.55). Targeted species constituted an average of 65% (n=9) and 71% (n=4) on protected and unprotected sites, respectively. Nontargeted species (graysby, *Epinephelus cruentatus*, coney, *E. fulvus*, rock hind, *E. adscensionis*, red hind, *E. guttatus*, and Nassau grouper, *E. striatus*) constituted on average 35% and 29% of the total number of individuals on protected and unprotected sites, respectively. Nassau grouper constituted a greater proportion of the individuals observed at protected (15%) than at unprotected (2%) sites. These values were statistically different (t=2.46, P<0.05).

Patch reefs protected from spear fishing had a significantly greater size of targeted individuals than did unprotected patch reefs ($F_{1,211}$=3.874, P=0.05). The mean size (+/– 1 SE) of targeted grouper species on protected patch reefs was 29.3 (0.7) cm, whereas the mean size of targeted species on unprotected sites was 26.0 (0.8) cm. There was also a significant difference among sites nested within protection levels ($F_{11,211}$=5.151, P<0.001).

Discussion

In this study, spear fishing appears to primarily influence the average size of groupers. Sites in which spear fishing was not allowed had grouper assemblages that were characterized by larger-size individuals. This result is similar to those found in studies examining the effects of hook-and-line fishing, where fishermen target the larger individuals in a population and thus decrease the average size of a fish species (Roberts and Polunin, 1991). Overall, grouper species composition was not significantly influenced by the presence or absence of spear fishing; targeted species were similarly abundant on protected and unprotected patch reefs. Sluka and Sullivan (1996) have shown that grouper species, such as black grouper, red grouper, and Nassau grouper, are more abundant, but smaller, on inshore patch reefs than on offshore bank reefs of the upper Florida Keys. It is likely that species such as these are recruiting inshore before they move offshore (Ross and Moser, 1995). Nassau grouper, however, were more abundant on patch reefs protected from spear fishing than on unprotected patch reefs. Although there is a ban on harvesting these species, spear fishermen may still collect individuals. It is important to examine how effective the ban on harvesting this species is in the Florida Keys.

Offshore bank reef sites in the upper Florida Keys protected from spear fishing had snappers (Lutjanidae) and grunts (Haemulidae) of larger size and greater abundance than did a lower Keys site subjected to spear fishing (Bohnsack, 1982). Clark et al. (1989) found similar results when sites inside Looe Key National Marine Sanctuary (lower Florida Keys) were compared before and after protection from spear fishing. The present study did not examine differences in abundance between protection levels. However, it is expected that there would be no significant differences in abundance between these sites; this result is due to the nature of both spear fishing and grouper growth and reproductive characteristics. Spear fishing targets the largest fish in an assemblage but only accounts for a small percentage of the total fishing effort (PDT, 1990). For example, spear fishing accounted for 10.5% of the total recreational fishing catch in Biscayne National Park.[1] Thus the magnitude of the selection pressure is likely much less than that from hook-and-line fishing because of

[1] Tilmant, J. T., and R. Stone. 1984. Reef fish harvest trends, Biscayne National Park, Dade County Florida. Unpublished report presented to the 1984 stock assessment workshop. Southeast Fisheries Center, National Marine Fisheries Service, Miami, Florida, 26 p.

the smaller number of spear fishermen. However, the lower number of spear fishermen may exert a more directed selectional effect on grouper species because they can be highly selective for the largest individuals.

The growth and reproductive characteristics of groupers render these species especially susceptible to overfishing (Bannerot et al., 1987; Shapiro, 1987; Huntsman and Schaaf, 1994). Groupers that are targeted by fishing grow slowly to a large maximum size (Manooch, 1987). The removal of larger individuals leaves behind smaller individuals to spawn. Over many generations, this can result in a decrease in the size and age at sexual maturity (Ricker, 1981) and also decrease the average size of the population (Roberts and Polunin, 1991). Many grouper species are protogynous hermaphrodites, changing sex from females to males later in life (Shapiro, 1987). Larger groupers are generally males, and at intensive fishing levels, the number of males in the population can be drastically reduced. If too many males are removed, sperm are reduced for reproduction (Bannerot et al., 1987). If sperm are reduced, protogynous stocks are more vulnerable to overfishing than are gonochoristic stocks (Huntsman and Schaaf, 1994). Species that are protogynous may experience a drastic reduction in reproductive capacity, even at moderate levels of fishing (Huntsman and Schaaf, 1994). However, there may be mechanisms by which the population can compensate for a changing sex ratio in the presence of overfishing (Claro et al., 1990; Huntsman and Schaaf, 1994). Huntsman and Schaaf (1994) showed that these types of compensation mechanisms can reduce the detrimental impacts of fishing pressure on protogynous species. In addition to protogyny, the reproductive behavior of groupers may increase their susceptibility to overfishing. Many species of grouper aggregate to spawn during one or two months of the year (Smith, 1972; Shapiro, 1987; Claro et al., 1990). These spawning aggregations are subject to intense fishing pressure (Olsen and LaPlace, 1978, Claro et al., 1990; Sadovy, 1994). In many parts of the Caribbean, aggregations have disappeared as a result of overfishing (Sadovy, 1994). Sluka et al. (1997) showed that reproduction (the total number of eggs produced per hectare) was six times greater in a marine fishery reserve in the central Bahamas than in the surrounding unprotected region.

It is concluded that the ban on spear fishing in the upper Florida Keys has significantly benefitted the size distribution of groupers. However, it appears that a ban on spear fishing alone has not resulted in recovering population levels of grouper in this region. Bohnsack et al. (1994) has clearly shown a decline in commercially and recreationally targeted grouper landings throughout the Florida Keys. Sluka and Sullivan (1996) have shown that the offshore grouper assemblage over shallow bank reefs of the upper Florida Keys is dominated numerically by graysby (88%), a small, nontargeted species. Densities of targeted species are low compared with regions where fishing was prohibited or had not yet taken place (Sluka and Reichenbach, 1996; Sluka et al., 1997).

It is recommended that marine fishery reserves be considered as a management measure because of their success in other regions and because of a strong theoretical basis (PDT, 1990). Grouper assemblages inside marine fishery reserves are more dense, of greater average size, and produce greater numbers of eggs per hectare than in similar, unfished sites (Bohnsack, 1982; Russ and Alcala, 1989, Roberts and Polunin, 1993; Watson and Ormond, 1994; Sluka et al.,1997). Although management measures, such as bans on spear fishing, have some beneficial effects, the available evidence suggests that the establishment of marine fishery reserves is the most successful method for restoring and conserving grouper assemblages.

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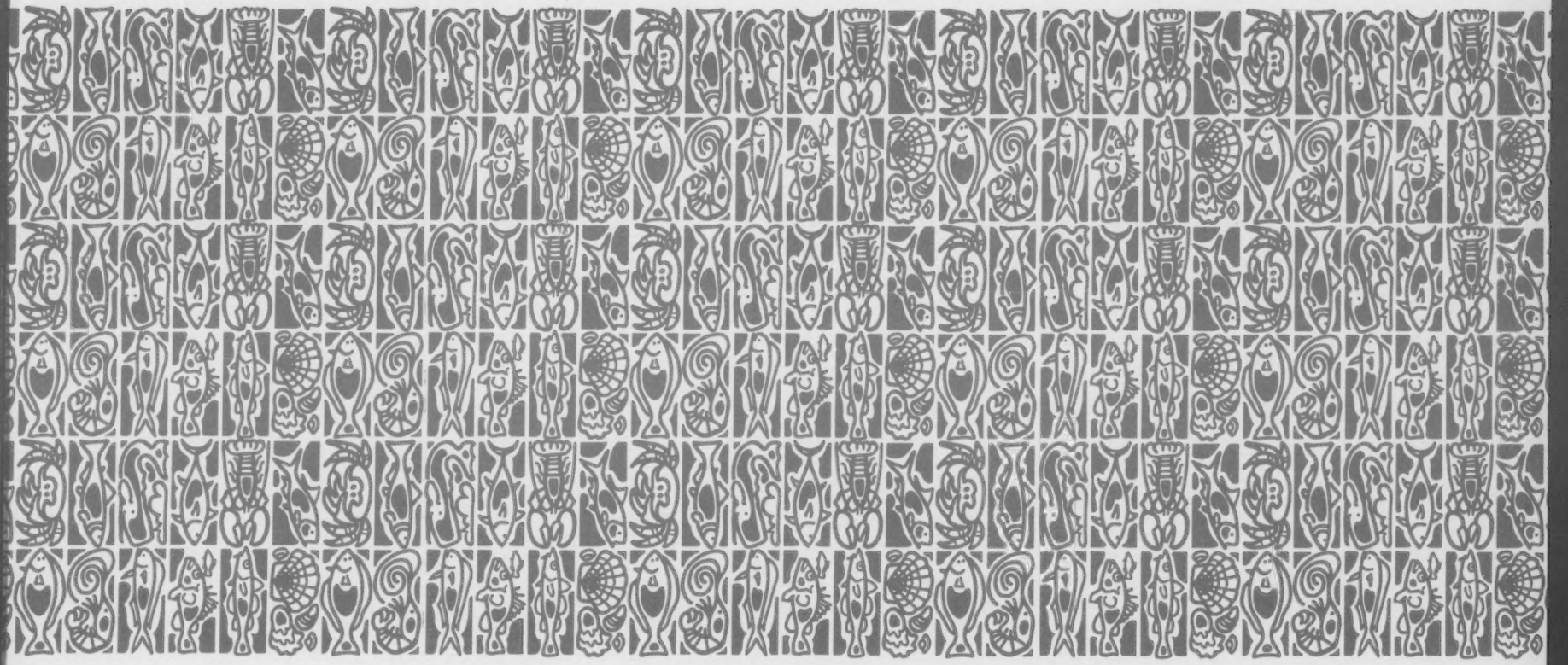
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